Wood-pasture diagnostics

Ecosystem services, restoration and biodiversity conservation

Pablo Garrido
Faculty of Forest Sciences
School for Forest Management
Skinnskatteberg

Doctoral thesis
Swedish University of Agricultural Sciences
Skinnskatteberg 2017

Acta Universitatis agriculturae Sueciae
2017:97

Cover: *Dehesa* wood-pasture landscape in Spain and detail of Gotland Russ grazing in Sweden
(photo & art: Pablo Garrido)

ISSN 1652-6880
ISBN (print version) 978-91-7760-084-8
ISBN (electronic version) 978-91-7760-085-5

Print: SLU Service/Repro, Uppsala 2017

Wood-pasture diagnostics. Ecosystem services, restoration and biodiversity conservation

Abstract

Wood-pastures are multi-functional habitats that uphold high ecological and cultural values. However, they are currently declining in Europe as a result of land use changes. How can we better understand wood-pastures to foster conservation?

To answer the question it is necessary to investigate both the social and ecological components of wood-pastures. Ecosystem services assessments have been dominated by biophysical and economic valuation approaches, while qualitative socio-cultural valuations are not commonly applied and therefore important services to people fail to be captured. To this end, a cross-site comparison of stakeholder perspectives in Sweden and Spain was applied here. This approach allows to additionally explore particular services and to identify current challenges for wood-pasture conservation.

In Sweden, most valued services were related to landscape beauty and recreation and eco-tourism, as well as pastures and biodiversity. In contrast, Spanish respondents perceived additional cultural services such as sense of place and identity values, traditional knowledge, cultural landscape and heritage values. Such similarities and differences might be explained by space and place theories of human-landscape relationship. Wood-pasture *dehesas* may then be perceived as places since people live within a wood-pasture matrix, and therefore have created associated values and social identities to the landscape transforming wood-pastures into places.

Swedish respondents identified the abandonment of wood-pastures and lack of new entrants into farming as major challenges for landscape and biodiversity conservation. To test potential new alternatives for wood-pasture restoration and management a field exclusion experiment was applied, where horse stallions were introduced. Horses reduced forest structural diversity and affected tree composition via selective browsing, suggesting that they could restore and maintain wood-pastures in Sweden. Horse grazing changed the functional composition of grasslands which favored prostrate plant species, with high specific leaf area, characteristic of ruderal communities. Plant and pollinator species richness were significantly higher in grazed compared to ungrazed areas. Thus, the reintroduction of horses may mitigate current biodiversity declines and foster wood-pasture and semi-natural grassland conservation.

Keywords: browsing pressure, ecosystem services, forest structure and composition, functional traits, grazing, large herbivores, pollinators, semi-natural grasslands, species richness, wood-pastures

Author's address: Pablo Garrido, SLU, School for Forest Management,
P.O. Box 43, 739 21 Skinnskatteberg, Sweden

Wood-pasture diagnostics. Ecosystem services, restoration and biodiversity conservation

Sammanfattning

Skogsbetesmarker är multifunktionella miljöer som upprätthåller höga ekologiska- och kulturella värden. Arealen skogsbetesmarker minskar emellertid i Europa till följd av förändringar i det areella brukandet. Hur kan vi bättre förstå hur skogsbetesmarkerna fungerar för att främja dess bevarande?

För att kunna svara på den frågan är det nödvändigt att studera såväl både sociala- och ekologiska perspektiv av skogsbetesmarker. Biofysiska- och ekonomiska evalueringsmetoder dominerar ofta i utvärderingar av ekosystemtjänster, medan kvalitativa, socio-kulturella värderingar sällan värdesätts, vilket kan leda till att viktiga antropogena funktioner åsidosätts. I denna avhandling gjordes en jämförande analys mellan Sverige och Spanien av avnämarnas perspektiv på skogsbetesmarkernas ekosystemtjänster. Det möjliggjorde en kartläggning av vilka ekosystemtjänster som är viktiga för avnämarna och en identifiering av aktuella utmaningar för bevarandet av skogsbetesmarker.

I Sverige var de högst värderade tjänsterna främst relaterade till landskapets skönhet, rekreation och ekoturism, men även värdet som betesmarker och bevarande av biodiversitet värderades högt. I Spanien, däremot värderades andra kulturella tjänster, såsom en känsla av tillhörighet och identitet, traditionell kunskap, det kulturella landskapet och kulturarvet. Sådana likheter och skillnader kan förklaras med så kallade rymd- och plats teorier som förklarar förhållandet mellan människa och landskap. Spanska skogsbetesmarker, *dehesas*, uppfattas i högre grad som viktiga platser eftersom många människor fortfarande bor i dess närhet, och de har därmed skapat andra värden och identiteter knutna till landskapet. I Sverige framhåller informanterna övergivandet av skogsbetesmarker och bristande rekrytering av nya brukare som huvudsakliga utmaningar för landskapet och bevarandet av dess biodiversitet.

För att testa nya alternativ till restaurering och förvaltning av skogsbetesmarker utfördes ett fältexperiment bestående av uthägnader och inhägnader med hästar (hingstar) som betesdjur. Hästarnas bete begränsade skogens strukturella diversitet och påverkande sammansättningen av träslag, vilket indikerar att hästar kan vara användbara för att restaurera och underhålla skogsbetesmarker i Sverige. Hästarnas bete ändrade även den funktionella artsammansättning av gräsmarkernas växtsamhälle, och gynnade marknära arter med stor bladstorlek, något som är karaktäristiskt för ruderatmarker. Artrikedomen av såväl växter som pollinerande insekter var signifikant högre på betade ytor än på obetade. Resultaten visar att återintroduktion av hästar som betesdjur kan begränsa förlusten av biologisk mångfald och främja bevarandet av skogsbetesmarker och semi-naturliga betesmarker.

Nyckelord: buskbete, ekosystemtjänster, skogsstruktur och -sammansättning, funktionalitet, bete, stora herbivorer, pollinerare, semi-naturliga gräsmarker, artrikedom, skogsbetesmarker

Author's address: Pablo Garrido, SLU, School for Forest Management,
P.O. Box 43, 739 21 Skinnskatteberg, Sweden

Dedication

To humanity

"*The tendency nowadays to wander in wildernesses is delightful to see. Thousands of tired, nerve-shaken, over-civilized people are beginning to find out that going to the mountains is going home; that wildness is a necessity; and that mountain parks and reservations are useful not only as fountains of timber and irrigating rivers, but as fountains of life. Awakening from the stupefying effects of the vice of over-industry and the deadly apathy of luxury, they are trying as best they can to mix and enrich their own little ongoings with those of nature, and to get rid of rust and disease*"

Muir, 1901

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Garrido*, P., Elbakidze, M., Angelstam, P., Plieninger, T., Pulido, F. & Moreno, G. 2017. Stakeholder perspectives of wood-pasture ecosystem services: A case study from Iberian dehesas. *Land Use Policy*, 60, 324-333.

II Garrido*, P., Elbakidze, M. & Angelstam, P. 2017. Stakeholders' perceptions on ecosystem services in Östergötland's (Sweden) threatened oak wood-pasture landscapes. *Landscape and Urban Planning*, 158, 96-104.

III Garrido*, P., Edenius, L., Mikusinski, G., Skarin, A., Jansson, A. & Thulin, C-G. Novel wood-pasture restoration and management alternatives: an experimental approach (manuscript)

IV Garrido*, P., Mårell, A., Ökinger, E., Skarin, A., Jansson, A. & Thulin, C-G. Grazing by semi-feral horses mitigates the effect of abandonment on plant community composition and pollinator habitat use (manuscript)

Papers I-II are reproduced with the permission of the publishers.

* Corresponding author.

The contribution of Pablo Garrido to the papers included in this thesis was as follows:

I Main author. Designed the study and collected the data. Translated and analysed the data. Wrote the manuscript together with TP and with contribution from co-authors

II Main author. Designed the study together with co-authors. Collected the data with field assistant. Analysed the data. Wrote the manuscript with contribution from co-authors

III Main author. CGT, AJ, AS, and LE set up the experiment. PG designed the study and collected the data. PG analysed the data and wrote the manuscript together with GM and contribution from co-authors

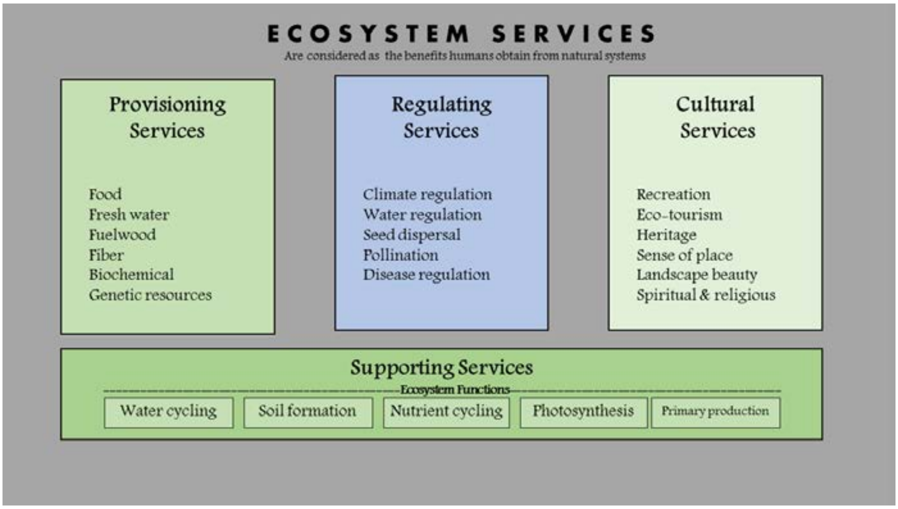
IV Main author. CGT, AJ, AS, and EÖ set up the experiment. PG prepared and compiled the data. PG designed the study together with AM. PG analysed the data and wrote the manuscript with contribution from co-authors

1 Introduction

Terrestrial ecosystems are largely modified by humans (Foley et al., 2005). This transformation has created diverse cultural landscapes (Tieskens et al., 2017), which can be significantly different in terms of structure and composition but provide valuable cultural services and support high levels of biodiversity (Tengberg et al., 2012, Fischer et al., 2012). Such landscapes resulted from long-term human nature interactions and thus contain important cultural heritage values (Plieninger and Bieling, 2012). Wood-pastures are cultural landscapes of particular interest due to their bio-geographical distribution and socio-ecological importance (Plieninger et al., 2015b). They have been an important part of European rural landscapes (Jørgensen and Quelch, 2014), and still cover about 203 000 km^2 in the EU27 (Plieninger et al., 2015b), concentrated mostly in Mediterranean and East European countries. In Europe, wood-pastures are historical management systems (Mosquera-Losada et al., 2009), characterized by scattered trees which provide shelter and forage for animals (Rackham, 2008, Costa et al., 2014), as well as a variety of by-products (e.g. firewood, charcoal, cork, fodder, acorns). Traditional management practices were characterized by multi-functional and extensive (cf. intensive agriculture) practices (Halada et al., 2011), implemented at varied temporal and spatial scales which fostered high biodiversity (Bugalho et al., 2011, Diaz et al., 2013, Torralba et al., 2016), and local ecological knowledge (Plieninger et al., 2015b). Wood-pastures have therefore been considered as high nature value farmland systems in Europe (Oppermann et al., 2012). However, they are severely threatened due to the effect of land use change modulated either by agricultural intensification or abandonment (Bergmeier et al., 2010), which entails great uncertainty for wood-pasture conservation and the services provided by interconnected human-nature interactions (Garrido et al., 2017b, Plieninger et al., 2015b). Further research is thus required for the successful conservation of wood-pastures in the long term, and constitutes the rationale behind the research presented in this thesis.

2 Connecting concepts and disciplines

Negative effects of human activities on nature and ecosystems were early emphasized (Marsh and Lowenthal, 1965). Hence, industrial societies began to realize the non-infinite nature of natural resources, and to evidence human induced consequences on natural capital and ecosystems (e.g., resource exploitation and pollution) (Braat and de Groot, 2012). Consequently, an increasing number of scholars started to capture ecological matters in economic terms, to highlight human societal dependence on ecological systems (Daily, 1997), and thus fostering biodiversity conservation concerns (Braat and de Groot, 2012). It is in this context when the term ecosystem services (ES) was coined (Ehrlich and Ehrlich, 1981) to connect the value of nature and ecosystems for human well-being (see Box 1). ES are generally defined as the benefits people obtain from ecosystems (MA, 2005). Therefore, ES can be understood as the link between the ecological and the social system (Díaz et al., 2011). However, ecological processes generating ES operate at different spatial scales. Thus, ES generated at a certain ecological scale (i.e., plant, plot, ecosystem, landscape, biome, globe) may benefit stakeholders at different institutional scales (i.e., local, regional, national, international level) (Hein et al., 2006). Each institutional scale comprises different stakeholders, whose interests might be conflicting (Tacconi, 2000). Stakeholders at local and regional level may ascribe different values to ES based on their cultural background and upon the impact of such services on their well-being (Hein et al., 2006). It is therefore crucial to consider different spatial and institutional scales on ES valuation since it may exert a significant effect on valuation results (Martín-López et al., 2009a). Human management decisions and practices are the result of the dynamic interaction of biophysical and sociocultural factors (Torralba et al., 2017), which in turn has an effect on the ecological system via land use and management practices (Díaz et al., 2011). Wood-pastures have been shaped by human activities and are therefore considered social-ecological systems (Plieninger and Bieling, 2012). They thus need continuous human management for their stability and are easily affected by socio-economic changes and subsequent management decisions altering their social-ecological resilience (Plieninger and Bieling, 2012, Plieninger and Bieling, 2013).



Box 1. Ecosystem services framework adapted from Millennium Ecosystem Assessment 2005.

ES in wood-pastures are frequently co-generated by natural processes in combination with human activities (Fischer and Eastwood, 2016, Palomo et al., 2016). Hence, they have been recently re-framed as social-ecological services (Huntsinger and Oviedo, 2014). Capturing aspects of human-nature co-production is important to avoid mistakes caused by narrow assumptions about “natural” systems, and to understand the need for multi-functional landscape management (O'Farrell and Anderson, 2010, Huntsinger and Oviedo, 2014). This is especially important in wood-pastures where management practices are needed to maintain the fragile ecosystem balance and the services produced by human-nature interactions. That fragile balance and the outstanding biodiversity levels of wood-pasture landscapes might be explained by the intermediate disturbance hypothesis (Marull et al., 2015).

Biodiversity, understood as the living components of ecosystems, is directly related to the provision of ES (Chapin III et al., 2000). Hence, biodiversity supports ecosystem functioning and the provision of services important for people and their well-being (Hooper et al., 2012, Cardinale, 2012). Simultaneously, stakeholder land use decisions favour or hamper certain organisms and their traits and therefore feed back onto the composition and functioning of ecosystems (Figure 1) (Díaz et al., 2011). The relative abundance, distribution, range and value of functional traits from the organisms that form certain ecosystem is referred to as functional diversity (Díaz et al., 2007). The functional traits of the organisms in an ecosystem, i.e., functional diversity, modulates ES delivery (Elmqvist et al., 2003, Kremen et al., 2007, de Bello et al., 2010).

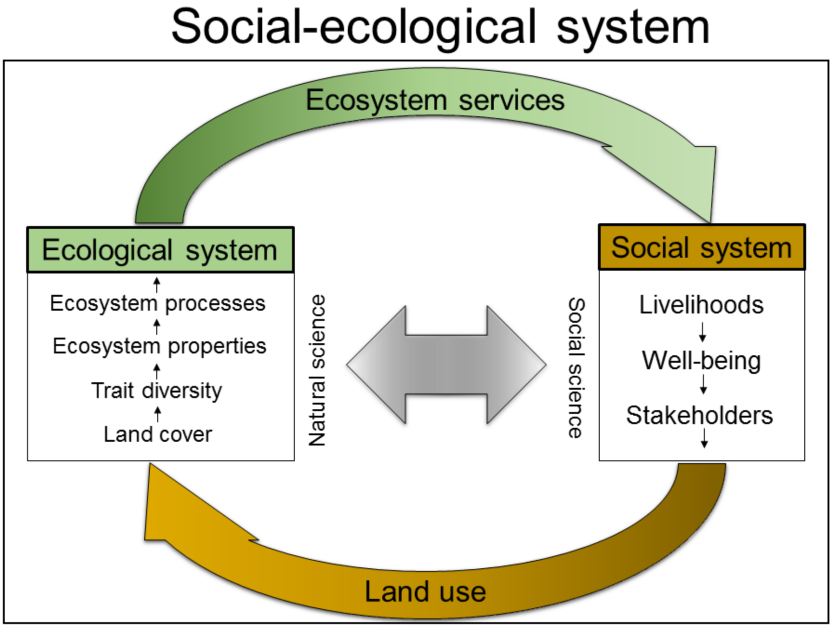


Figure 1. Conceptual framework to understand the interplay between the social and ecological system. Land use choices affects the ecological system and generate different land covers which favour or hamper certain organisms and therefore trait diversity. This in turn, feed back onto the composition and functioning of ecosystems and delivered services. The central arrow highlights the importance of combining social and natural sciences to better understand social-ecological systems. Adapted from Diaz et al. 2011.

For instance, different plant species comprise different functional trait values, which affect different ecosystem properties and therefore have different effect on the environment we live in. Nutrient and carbon cycling (Wardle et al., 2004), litter decomposition and productivity (Pérez-Harguindeguy et al., 2000, Lavorel and Garnier, 2002), plant-herbivore strategies (Díaz et al., 2001), and plant resistance to climate variability (Grime et al., 2008), are all regulating the ecosystem properties and thus the delivery of services to humans. Moreover, different stakeholders develop different strategies to secure their livelihoods and well-being. In order to obtain the ES needed to secure their livelihood strategies or well-being, they use and access ecosystems and their functional diversity in different ways. For instance, traditional farmers perceived wood-pastures as source of food, pastures for their livestock, fuel (e.g., firewood), and medicine

(Garrido et al., 2017b, Garrido et al., 2017a). They therefore highly value productive oaks to feed their swine herds (Parsons, 1962), the abundance of plants of high nutritional value for their livestock, and a diverse landscape that provides opportunities for different subsistence activities at different times of the year (Jørgensen, 2013, Davies and Watson, 2007). Due to their low-intensity multi-purpose management strategies, farmers practicing traditional management use a high number of ES and thus value the presence of a wide range of species of different biological attributes. Production oriented cattle ranchers who have simplified the traditional management, have specialized in the use of a small number of ES to sustain their production. They therefore value certain biological attributes for their commercial production and placed higher value on the abundance of high-quality grass fodder and neglect the properties and functions of other biological components since they are of no value to them. In times of fodder shortage they can supplementary feed the livestock and therefore they do not depend on a wide range of functional attributes and do not therefore value them. Crop production oriented farmers, prioritize a single ES, i.e., soil fertility, to maximize crop yield. This stakeholder group may not ascribe any value to any component of functional diversity as provider of ES. Indeed, any pre-existing natural or semi-natural vegetation is not contributing to their strategy and is therefore considered as an obstacle for their activity. Environmental NGOs and official authorities value wood-pastures as source of education, recreation and heritage values and thus appreciate all components of functional diversity with special emphasis on endemic, endangered or emblematic species (e.g., Iberian lynx (*Lynx pardina*) and Spanish imperial eagle (*Aquila adalberti*)) (Caro, 2010). Additionally, abundant organisms usually have higher impact on ecosystem properties than less common ones (Grime, 1998, Garnier et al., 2004), and therefore in wood-pastures, dramatic changes can be expected when for instance grazing as traditional management practice, cease (Paper IV). Understanding biodiversity through the functional traits of organisms that form an ecosystem clarifies the linkages between biodiversity and properties and processes that generate the ES important to support human life and well-being (Cadotte et al., 2011). This in combination with capturing the different stakeholder perspectives and values may help to better understand the social and ecological components of wood-pastures and therefore facilitate novel management alternatives for their conservation in the long term (Garrido et al., 2017a). Since stakeholders manipulate different land covers, functional diversity, and ecosystem properties to obtain particular combination of ES, to capture their perspectives is crucial. The impact at landscape level of decisions made by stakeholders will greatly depend on their relative political power and access to ecosystems (Díaz et al., 2011, Quétier et al., 2010).

3 Objectives

Wood-pastures are appreciated for biodiversity and cultural heritage values, but are threatened today by land use changes in the form of agricultural intensification or abandonment. Thus, the first aim of this thesis was to diagnose the status of wood-pastures and elucidate pressing current challenges for their long term persistence by applying a qualitative socio-cultural valuation of ecosystem services. This allowed for realising the second aim of the thesis namely to experimentally test potential alternatives for wood-pasture and semi-natural grassland conservation in Sweden.

The main questions were:

1. How the perception of services vary among different stakeholder profiles? Is the perception of services different at local and regional level? Which are key services for wood-pasture conservation? Are stakeholders from different countries perceiving ecosystem services differently? What are the pressing challenges for wood-pasture conservation? (Paper I and II)
2. Can wood-pasture abandonment in Sweden be tackled by introducing large herbivores? Is it possible to use Gotland Russ (*Equus ferus Caballus*) for wood-pasture restoration and management? Does horse browsing have an effect on the forest structure? What is the effect of browsing on the forest composition? Which trees are preferred by horses? (Paper III)
3. What are the effects of horse grazing on semi-natural grasslands? Can current biodiversity declines be mitigated through horse grazing? What is the effect on plant species richness? Can grazing have positive cascade effects on pollinators? (Paper IV)

4 Methods

4.1 Study areas

4.1.1 Cáceres province (Paper I)

Extremadura is a region located in southwestern Spain (ca. 39°N, 6°O) covering more than 40 000 km^2 (Ezquerra Boticario and Gil Sanchez, 2008). The total forest and woodland cover equals 16 000 km^2 of which 77% (12 370 km^2) correspond to oak wood-pastures called *dehesas* (Pulido et al., 2010), where the Cáceres province is at the center of its range and was therefore selected as the study area (Figure 2). Early signs of human forest opening by fire goes as far as 6 000 years back (López Sáez et al., 2007), although there is evidence of tree adaptation to fire (e.g., cork oak), suggesting a much longer co-evolution (Grove and Rackham, 2003).

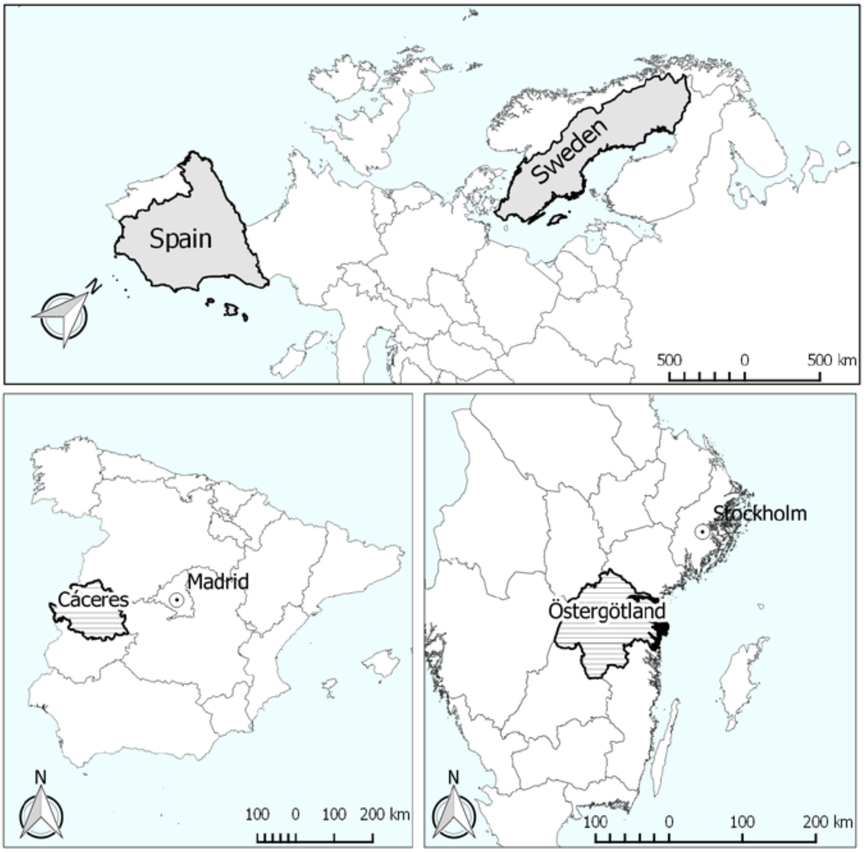


Figure 2. The location of both study areas: (Right) Östergötland County in Sweden with total cover of oak wood-pastures with high natural values equals 180 km^2; and (Left) Cáceres province in Spain where the total forest and woodland area equals 16 000 km^2 of which 77.3 % (12 370 km^2) correspond to *dehesas*. Sweden and Spain administrative borders were extracted from the GADM database (www.gadm.org), version 2.8, November 2015.

The *dehesa* is mostly privately owned by big estates (>100 ha). Tree species such as holm (*Quercus ilex*), cork (*Q. suber*) and Pyrenean oak (*Q. pyrenaica*) dominate the tree canopy of *dehesas*. Tree density varies (10-100 ha^{-1}) depending on land use (Moreno and Pulido, 2009). The trees are a fundamental component of the *dehesa* system, producing not only forage (acorns, fodder, browse), energy (firewood and charcoal), and cork, but also creating favourable micro-climatic conditions for herbaceous understory and providing shelter for livestock (Marañón, 1988, Joffre et al., 1988). The traditional multi-purpose land management has generated a mosaic of habitats with high plant species diversity both at local (Marañón, 1985, López-Sánchez et al., 2016) and landscape scales

(Moreno et al., 2016). The *dehesa* landscape has been fundamental for the regional rural economy (Campos, 2004), while simultaneously supporting high biodiversity values (Díaz et al., 1997, Olea and San Miguel, 2006) for which it has been included in the EU Habitat directive 92/43 (Costa et al., 2014) (Photo1).

Photo 1. Traditional *dehesa* where Iberian swine herds are free ranging feeding on acorn in autumn. Photo: Pablo Garrido.

There has been a transition from an agro-silvo-pastoral system, to a simplified wood-pasture during the last decades (Mosquera-Losada et al., 2009). Traditionally, native cattle breeds, merino sheep, goats and Iberian pigs were free ranging in *dehesas* (Marañón, 1988), and pig fattening with acorns was important for the agrarian economy (Parsons, 1962). Agricultural practices were performed in long rotation periods (3-12 years; depending on soil productivity), in combination with pruning and lopping activities of oaks to facilitate sunlight to reach the ground for agriculture and grassland development, and to maximize acorn production (Moreno and Pulido, 2009). These practices also prevented shrub encroachment and soil compaction. Seasonal herd movements (transhumance) were common, traditionally conveying more than 3 million sheep from the north to wintering areas in the southern part of the Iberian peninsula (Klein, 1920). These seasonal movements utilized a specific network for their migrations, known as drove roads (*cañadas*), that are today legally protected (Law 3/1995).

Currently, eco-tourism, bird watching and recreational big game hunting activities are gaining momentum on *dehesa* estates, while agricultural practices are becoming less central (see Paper I, Table 1). Particularly recreational hunting is today an important socio-economic activity for private *dehesa* estates after the abandonment of the traditional uses and rural depopulation (Olea and San Miguel, 2006, Moreno and Pulido, 2009). Today ranchers are mostly specialized in the production of single livestock species, i.e., cattle, sheep, goats, pigs and fighting cattle, although combinations commonly occur.

4.1.2 Östergötland County (Paper II)

In Sweden, the largest area of wood-pasture remnants is located in Östergötland County (Figure 2; Photo 2), where in total around 180 km^2 of valuable wood-pasture habitats persist scattered in small patches (CAB, 2005). They were traditionally used for animal husbandry, including grazing and hay-making (Jørgensen and Quelch, 2014).

Photo 2. Tinnerö *eklandslkap* in Ötergötland. Photo: Mikael Angelstam

Today, old sun-exposed pedunculated oaks (*Quercus robur*) located on wood-pastures host a high diversity of saproxylic beetles (Ranius et al., 2005), butterflies (Bergman et al., 2007) and lichen species (Paltto et al., 2010). Also, associated semi-natural grasslands are the most species-rich habitats in Sweden (Svensson, 1988). However, such wood-pastures are currently threatened by insufficient or non-existent traditional land management (Paltto et al., 2011), and are severely fragmented (Bergman et al., 2004). Moreover, due to changes in land use and the abandonment of agricultural practices these habitats have dramatically declined (SBA, 2005b, SBA, 2005a).

To understand the current distribution of oak habitats and wood-pastures in Sweden, it is important to consider both broad climatic drivers and historical facts (Eliasson and Nilsson, 2002, Lindbladh and Foster, 2010). During the 16th to 19th centuries, acorns were an important source of fodder for livestock, and timber was valuable in the agrarian economy. Simultaneously, oak timber was a strategic resource for warships construction by the Swedish state. Hence, to ensure the preservation of oak trees, in 1558 the oak was declared property of the Swedish state by King Gustav Vasa. This decision had adverse consequences for farmers since the use of oaks was no longer allowed and thus oak became an impediment for agricultural development. As a consequence a large proportion of oaks were deliberately damaged. This conflict of interest between the state and local farmers escalated during the following centuries and created a widespread hatred toward oaks. This lasted until 1830 when royal ownership of oak ceased. A consequence of this oak hatred was a significant reduction of oak trees due to intense harvesting by local farmers (Eliasson and Nilsson, 2002). In contrast, nobility could afford to preserve the oaks within their estates. By the 19th century the oak occurrence had been reduced dramatically to current levels (Eliasson and Nilsson, 2002, Lindbladh and Foster, 2010).

Wood-pasture restoration (i.e. removal of competing secondary woodland trees and introduction of livestock to maintain the open woodland character through grazing) has been implemented in order to restore the biodiversity and cultural values associated with wood-pasture landscapes. Core areas for oak habitat conservation have been identified based on the hermit beetle (*Osmoderma eremita*) requirements as focal species (see Paper II, Figure 1); these habitats are also included in the EU Habitat directive 92/43.

4.1.3 Krusenberg (Paper III and IV)

Krusenberg is an estate of 842 ha located 17 km south of Uppsala (Sweden), owned and managed by the Swedish University of Agricultural Sciences (Figure 3a). The property contains 204 ha of agricultural land, 72 ha of pasture and grasslands, 510 ha of forest and, 46 ha correspond to other land uses (Päiviö, 2008). The forest land is dominated by coniferous species (71 %) interspersed with coniferous forest on lichen-dominated (12 %), dry (6 %), and wet areas (2 %). Broad-leaved-coniferous (mixed) forest, and broad-leaved forest also occur. The area is located within the Hemiboreal zone (Ahti et al., 1968). Mean temperature over the study period corresponded to -4.8 °C (±6.5 SD) in January and 17.5 °C (±4.1 SD) in July, while precipitation in July ranged between 65 mm and 123 mm. From 2004 to 2014 (i.e., the beginning of the experiment), pasturelands have not been tilled, and were occasionally harvested and/or grazed. During the growing season, the experimental area, including forest land, has been grazed by cattle in unknown numbers (Ryberg, pers.comm.).

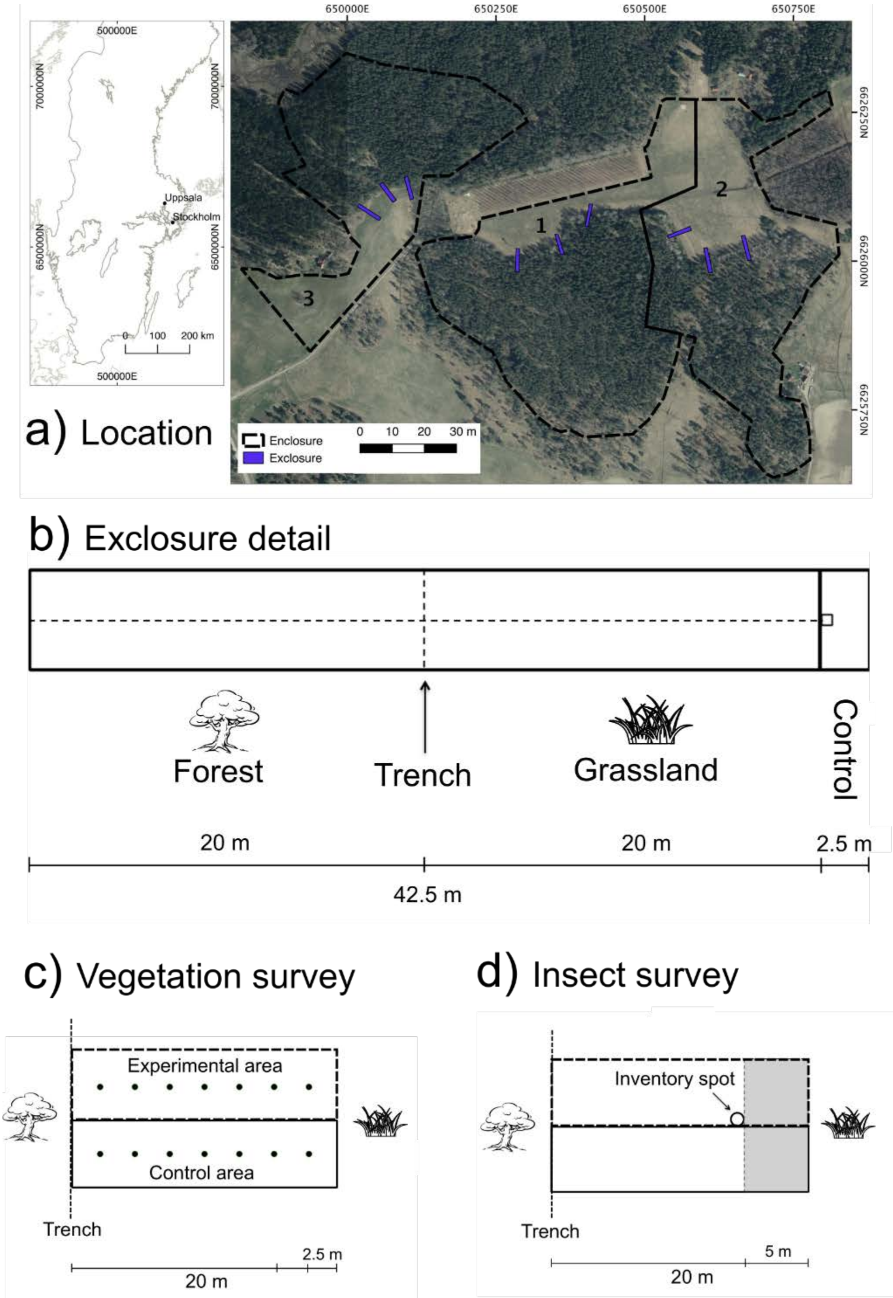


Figure 3. a) Location of the study area and experimental design at Krusenberg estate in southwestern Uppsala (Knvista), Sweden. © Lantmäteriet. b) Design of each herbivore exclosure (control area). c) Vegetation survey design. Seven paired permanent control and experimental plots ($0.25m^2$) were surveyed. d) Butterfly and bumble bee survey design, where the area surveyed is shaded in grey, adapted from the Swedish Butterfly Monitoring Scheme.

4.2 Wood-pasture diagnostic methods (Paper I and II)

4.2.1 Stakeholder sampling

A stakeholder is considered as a person or group that has an interest in something, in this case in wood-pastures. To characterize the different stakeholder profiles of the study areas, stakeholder categories were first identified by communication with experts and official authorities. The selection of respondents was attained through snowball sampling (Atkinson and Flint, 2004). They were later grouped according to the sector they represented, i.e., civil sector, including non-governmental organizations and civil associations, private sector, comprising businesses controlled or owned by private individuals, and public sector respondents, which were represented by governmental agencies and local governmental units. They were additionally categorized by their level of governance or institutional scale in either local or regional level; important to implement cross-scale assessments (Ribeiro et al., 2016). This sampling strategy resulted in a total of 29 respondents in Sweden, and 34 in Spain (see Paper I, Table 2; Paper II, Table 1).

4.2.2 Socio-cultural valuation of ecosystem services

Ecosystem services research is increasingly used in environmental policy and practice (de Groot et al., 2010a, Gómez-Baggethun et al., 2010), and has proven useful to stress changes in ecosystems and to identify priority areas for implementing the wider political agenda (MA, 2005, TEEB, 2010). Three main approaches have been utilized in ES research including biophysical, socio-cultural and economic (de Groot et al., 2010b). However, in practice ES research has focused predominantly on biophysical and economic assessments (Vihervaara et al., 2010). In contrast, efforts to characterize cultural services have been neglected due to the difficulty to capture intangible aspects (Satterfield et al., 2013, Chan et al., 2012b, Daniel et al., 2012, Chan et al., 2012a, Blicharska et al., 2017). These aspects, however, are of paramount importance for a successful implementation of management strategies (Mascia et al., 2003, Ban et al., 2013).

Most studies analysing ES demands from stakeholder perspectives have been performed at the local level and have focused on a few services and narrow stakeholder profiles (Martín-López et al., 2012). While some research on socio-cultural valuation of ES has recently emerged (Villamor et al., 2014, Scholte et al., 2015, Oteros-Rozas et al., 2014), there is a need for qualitative assessments to widen valuation methods of ecosystem services (Fagerholm et al., 2016).

Qualitative approaches “interpret phenomena in terms of the meanings people bring to them” (Denzin and Lincoln, 2011), and are therefore fundamental to articulate the expression of services and values important to people (Chan et al., 2012b, Chan et al., 2012a). For a holistic understanding of the studied wood-pasture landscapes a case study approach was applied (Flyvbjerg, 2011) and for a full characterization of services, a qualitative socio-cultural assessment of ecosystem services (see Appendix 1 for Questionnaire). The responses were translated into ES categories (MA, 2005) (see Box 1). The themes that emerged during the analysis were coded and grouped into main categories. To identify how ES were addressed in the interviews an Ecosystem Service Coding Protocol (CP) was applied (Wilkinson et al., 2013). This allowed for consistence of coding among all analysed interviews. The CP included four categories of services: supporting (coded A), provisioning (B), regulating (C) and cultural services (D) (MA, 2005). Additionally, each category contained a number of ES (see Paper I, Table 3; Paper II, Table 2).

4.3 Field experimental approach: the treatment (Paper III and IV)

4.3.1 Experimental design

A three year field experiment with paired control and experimental plots was applied at three different 13, 11 and 10 ha wood-pasture enclosures. Control plots mimicked land abandonment conditions, while experimental plots the restoration of wood-pastures and semi-natural grasslands by a known stocking rate of large herbivores. Along the edge zone of each enclosure, three rectangular 40 x 5 m (20 m into the forest and 20 m into the grassland) exclosures (controls) were placed to simulate abandonment conditions in May 2014 (Figure 3b). Four free-ranging one-year-old horse stallions were released per enclosure, where they were kept without supplemental feeding for three growing seasons till September 2016. Although the experimental design might have allowed wild herbivores (e.g., rodents, hares, roe deer and moose) access the exclosure areas, their effect was considered negligible (Photo 3). The study was performed using a cross-over design where the horse groups were shifted between enclosures once a year. The body condition of horses were scored every week according to Henneke et al. (1983), and horses that scored < 4 (4 equals “moderately thin”) were temporarily removed from the enclosures and offered additional pasture or were supplementary fed. During the study period, four individuals were temporarily removed due to low body condition in late winter.

Remains of wild horses dated to 11 200-10 400 years before present (YBP) have been found in southern Sweden (Liljegren and Ekström, 1996). The oldest finding suggested to be a domesticated horse, have been found in Gotland, dated to 4700 YBP (KSLA, 1998). Although this horse might have been domesticated, free-ranging horses have been present on Gotland until the 20th century (Ljunggren, 1967). Feral horses are mentioned in the literature from the 13th century and, when Carl Linnaeus visited Gotland in 1741, he described traps made to capture horses (von Linné, 1745). The last known hunt for horses on Gotland was in 1932 (Norrby, pers. comm.). Because of the feral history of the breed, it may have retained a sufficient rustic character (e.g., energy retaining characteristics and feeding behavior) to serve as a tool for wood-pasture restoration and management, while fostering the conservation of a critically endangered national breed; liability commissioned by FAO (First report on the state of the world's animal genetic resources), according to which Sweden is obliged to preserve the breed.

Photo 3. Effects of grazing and browsing on experimental and control areas at Krusenberg estate in 2016. Photo: Pablo Garrido.

4.3.2 Vegetation surveys and plant traits

For tree vegetation, the total number of trees was counted at paired control-experimental plots in 2016 (Figure 4). Trees taller or equal to 20 cm (minimum browsing height for large herbivores; Nichols et al., 2015) were identified to species level (besides *Salix* spp.) and selected for the study. Tree height (cm), diameter (cm), total number of twigs, and total number of browsed twigs were recorded per selected tree. Additionally, trees were also categorized into height classes; class 1, trees up to 3 m, class 2 included trees from 3 to 5 m, and class 3 corresponded to trees higher than 5 m. Diameter of class 3 tree individuals were taken at breast high (dbh; 1.30 cm); few centimeters from the ground otherwise.

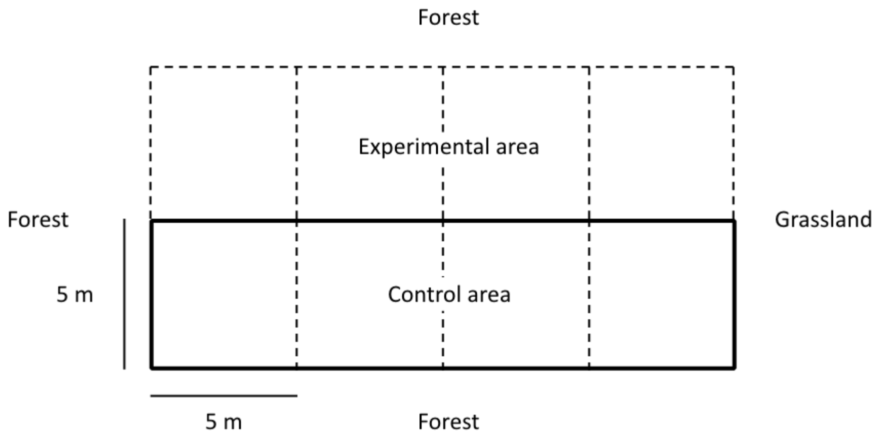


Figure 4. Detail of study design

For grassland vegetation, seven circular plots of 0.25 m^2 (0.282 m radius) were placed equidistant 2.5 m at paired control-experimental plots (Figure 3c). Vegetation surveys were performed in July and September 2014, and May, July and September 2015 and 2016. Permanent plots were marked with black plastic needles hammered into the soil. For each plot, all plants were identified at species level and their abundance recorded. Grasses were registered as a group, including *Alopecurus pratensis*, *Festuca rubra*, *Dactylis glomerata*, *Phleum pretense*, *Festuca pratensis*, *Poa annua*, *Lolium perenne*, *Elytrigia repens*, *Agrostis gigantean*, *Agrostis capillaris*, *Deschampsia cespitosa*.

To understand the effects of grazing on plant ecological strategies (Grime, 1977), plant-herbivore interactions, biodiversity and ecosystem functioning, functional trait-based approaches have recently emerged (de Bello et al., 2005, Laliberte et al., 2012, Violle et al., 2007). Plant functional traits can therefore facilitate the understanding of the mechanisms modulating plant responses to grazing. For instance, leaf N content and specific leaf area (SLA) are traits closely associated to growth rate (Wright et al., 2004), as well as to plant tolerance strategies to herbivory (Strauss and Agrawal, 1999, Díaz et al., 2001).

In order to understand the response of plants to biotic and abiotic factors, three plant ecological strategies were proposed (e.g., Grime, 1977): plants adapted to (i) low stress and low disturbance levels (competitive plants; C), (ii) high stress and low disturbance (stress-tolerant; S), and (iii) low stress and high disturbance levels (ruderal plants; R). However, limitations to the applicability of the CSR scheme has been argued due to axes' definitions based on reference concepts and, therefore LHS plant ecology scheme was also included (Westoby, 1998). This scheme comprise specific SLA (mm^2 g^{-1}), plant height at maturity (H; cm), and seed mass (SeedMass; g). LHS data was compiled from the LEDA plant trait database (Kleyer et al., 2008), and CSR trait data from Hunt (Hunt et al., 2004) and the BiolFlor database. Based on the species-specific trait values obtained, community weighted mean (CWM) values were derived for each plant trait (Lavorel et al., 2008). Since a parallel decline of plants dependent on insect pollination for reproduction have been reported (Biesmeijer et al., 2006, Carvalheiro et al., 2013), plants dependent on different pollination mode vectors were also categorized. To assign plant pollination mode vectors to the plant pool data, the BiolFlor database and the flower classification from Mueller (see Klotz et al., 2002) was used. Plant species were classified as bee, generalist and wind pollinated (see Paper IV, Appendix 1 for details).

4.3.3 Pollinator surveys and traits

Biodiversity conservation management strategies for grasslands have primarily been targeting vascular plants (WallisDeVries et al., 2002, Tälle et al., 2016), while plant-pollinator interactions are equally fundamental for the stability and functioning of ecosystems and intrinsically connected to changing land use practices (Kremen et al., 2007, Aslan et al., 2013). Therefore, flower-visiting species such butterflies and bumble bees, should be monitored for improving the understanding of how management practices affect biodiversity and the functioning of ecosystems (van Klink et al., 2015). Butterflies and bumble bees are both key pollinator groups with differing co-evolutionary relationship with plants (Alanen et al., 2011). They have additional specific properties that qualify them as suitable complementary taxon for biodiversity conservation assessments. They are well-studied compared to other taxonomic groups (Boggs et al., 2003), have shown to have a rapid response to environmental changes (Goulson et al., 2005, Thomas et al., 2004), and may be used as umbrella species for other insect taxa (Thomas, 2005). For butterflies and bumble bees, a point inventory method developed by The Swedish Butterfly Monitoring Scheme was applied. Each paired 5 x 5 m experimental and control plot was observed for 20 minutes twice a day (Figure 3d) and three times a year in 2016. Surveyed areas were observed depending on sunlight and solar time; criteria described in the National Inventory of Landscapes in Sweden (NILS), i.e., at least 17°C and preferably sunshine, particularly for butterflies (Cornvall, 2017). Total number of species in paired grazed and ungrazed plots were recorded.

Life-history traits can be used to assess changes of insect communities in response to environmental changes. For instance, niche breadth is a key ecological characteristic determinant of species distribution and abundance in fragmented landscapes (Ewers and Didham, 2006), and suggested to explain sensitivity to land use changes (Moretti et al., 2009). For bumble bees, niche breadth can be characterized by proboscis length, being long tongued bees more specialized in foraging long corolla tube flowers (Goulson, 2003). For butterflies, it can be defined by larval-plant specificity feeding habits (Komonen et al., 2004) and larval host plant specialization (Alanen et al., 2011). Butterfly species were classified as host-plant specialist when butterfly larvae fed on plants belonging to a single plant genus, or generalist when feeding on at least two species belonging to different plant genera (Öckinger et al., 2010). For bumble bees, species were classified as having long or short proboscis. Long-tonged species denote a higher degree of flower forage specialization (Ødegaard et al., 2015, Cederberg and Mossberg, 2012)(see Paper IV, Appendix 2 for details).

4.4 Statistical analyses

4.4.1 Quantitative estimates of tree selection (Paper III)

In order to elucidate whether the experimental horse breed could be used as tool for wood-pasture restoration and management, it is important to quantify the browsing pressure exerted on different tree species and to estimate tree preferences. In this thesis, browsing pressure was investigated up to three meters; i.e. the browsing height for moose (*Alces alces*) (Bergström et al., 1995) and assumed to be the maximum reachable height for horses (height at withers around 115-130 cm). Browsing pressure per tree was calculated as the ratio between the number of browsed twigs divided by the total number of twigs per tree. To generate quantitative estimates of tree selectivity, a general model was applied (Chesson, 1978, Greenwood and Elton, 1979, Månsson et al., 2007). This consisted in three different parameters:

$$ui = \frac{viai}{\sum_{i=1}^{I} viai} \qquad (1)$$

where *ui* is the relative proportion of utilized food item *i*; based on browsing pressure estimates per individual tree species, *v* corresponds to a selectivity parameter, *a* refers to the proportion of available food item *i*; computed as the number of trees of species *i* divided by the total number of trees per plot, and *I* represents the total number of tree species considered; including Scots pine

(*Pinus sylvestris*), silver birch (*Betula pendula*), European ash (*Fraxinus excelsior*), aspen (*Populus tremula*), blackthorn (*Prunus spinosa*), pedunculate oak, sallow (*Salix* spp.) and rowan (*Sorbus aucuparia*). Pine was considered as representing the minimum number of observations to ensure sufficient statistical power (i.e., 41), and thus species with lower occurrences were excluded as well as Norway spruce (*Picea abies*) due to herbivory avoidance (see Paper III, Table 1). Availability of tree species was calculated based on the selected eight tree species per plot. Trees up to five meters were included in the analysis; higher trees (class 3 category) were excluded due to limited effect of browsing on tree survival.

To find the selectivity parameter *v* for each tree species eq. 1 can be re-organized so that

$$vi = \frac{ui}{ai \sum_{i=1}^{I}(ui/ai)} \qquad (2)$$

since the relative proportion of utilized tree species *u* sum to 1. One of the strengths of the model is the possibility to compare selectivity parameters for different tree species. However, this index is not normally distributed (Månsson et al., 2007) and therefore a log transformation is suggested (Aitchison, 1986).

$$xi = ln\left(\frac{vi}{v0}\right) \qquad (3)$$

where *vi* represents the selectivity parameter for the tree species *i*, and *v*0 denotes the selectivity parameter of the reference species; in this case pine.

4.4.2 Grazing effects on grasslands and pollinators (Paper IV)

Generalized linear mixed models (GLMM) were used, due to the hierarchical structure of the experimental design where plots were nested within exclosures and these within enclosures (Bolker et al., 2009, Zuur et al., 2009). GLMMs were fitted to a Gaussian, Poisson or Binomial distributions, including a nested random structure conditioned by the hierarchical experimental design. Additionally, butterfly and bumble bee data was collected twice a day and three times a year and therefore a particular method to handle the repeated measurement nature of the data was used. For this a GLMM using a penalized quasi-likelihood (PQL) method was applied (McCulloch and Neuhaus, 2001, Breslow and Clayton, 1993).

First, whether plant species richness was affected by the experimental treatment (grazed vs. ungrazed) and time was investigated. GLMMs were used with a nested random structure term; plot within exclosure and enclosure, and season, fitted to a Poisson distribution (log-link). Then, the relative proportion of bee, generalist and wind pollinated plants was calculated to test for effects of treatment and year. GLMMs with a nested random structure term; plot within exclosure and enclosure, and season, fitted to a Binomial distribution (logit-link) were used. The relative abundance per plot of the response variables was used as weights in the model.

Secondly, CWM traits as a measure of functional composition (Laliberte et al., 2012) were applied. CWM were computed as the weighted trait mean per plot, where weight corresponded to the species relative abundance. CSR and LHS (log-transformed) CWM traits and principal component analysis (PCA) to visualize the grassland community changes induced by treatment through time were used. Then the effect of the CWM trait values on the experimental treatment trough time was tested by fitting the CWM trait values to a GLMM with a nested random structure term, plot within exclosure and enclosure, fitted to a Gaussian distribution.

Finally, butterfly and bumble bee species richness and behavior (feeding-resting) was investigated in grazed compared to ungrazed conditions. For this purpose only data on pollinators from 2016 was employed in order to test for the cumulative effect during the three year experimental time. GLMM-PQL models were used due to the repeated measurement nature of the butterfly data, with a nested random structure term, i.e., plot and treatment within enclosure and date, fitted to a Poisson distribution. The effect of butterfly and bumble bee species richness and behavior on butterfly host plant specialization traits and, on bumble bee proboscis length trait was also tested. For more details on statistical packages, models and literature references for statistical analyses see Appendix 3 in Paper IV.

5 Results and discussion

5.1 Wood-pasture diagnosis (Paper I and II)

5.1.1 Cross-site comparison of stakeholder perspectives

In Spain, stakeholders acknowledged a total of 45 ecosystem services (Paper I). In contrast, 34 services were acknowledged by Swedish respondents (Paper II). At local level, cultural services were the most commonly perceived services in Sweden while provisioning services were highlighted the most in Spain (Figure 5a,b). Among cultural services, stakeholders from both regions acknowledged recreation and eco-tourism services associated with wood-pastures (see Paper I, Table 3 and Paper II, Table 2). Additionally, cultural landscape and landscape beauty were identified as important in Sweden, whereas in Spain respondents additionally highlighted traditional knowledge and heritage values. Provisioning services included livestock and pastures and, to a lesser extent timber and crops were also indicated in Sweden. In Spain, livestock and pastures were also the most mentioned provisioning services at local level, followed by fodder from trees, firewood, charcoal, wild game and other sub-products such as cheese, olive oil, sausages, and wine. Regarding supporting services, both Swedish and Spanish respondents appreciated biodiversity. In Spain, respondents additionally acknowledged water cycling, nutrient cycling and photosynthesis. Regulating services were rarely expressed by stakeholders in Sweden; the only two services mentioned were noise regulation and water regulation and purification. The variety of services perceived by Spanish respondents was much greater, and natural hazard regulation, in particular fire prevention, was the most frequently acknowledged. Seed dispersal, erosion regulation and climate regulation were also mentioned.

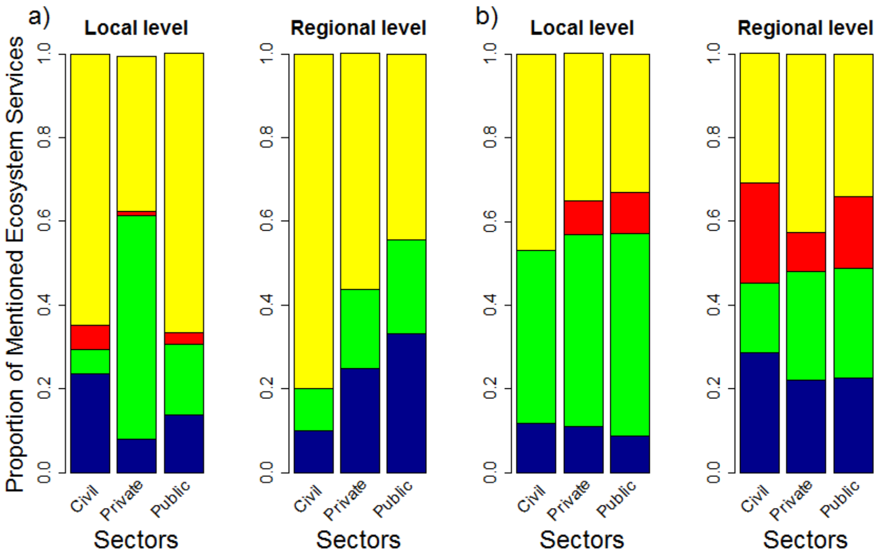


Figure 5. Ecosystem services from wood-pasture landscapes mentioned by stakeholders from different sectors at local and regional level in a) Östergötland County (Sweden), and b) Cáceres province (Spain). Yellow-cultural, red-regulating, green-provisioning, blue-supporting services.

At regional level, both Swedish and Spanish respondents valued cultural services the most (Figure 5a,b). Swedish mostly mentioned recreation and eco-tourism services, landscape beauty and education and knowledge. Spanish appreciated most frequently education and knowledge services, traditional knowledge, cultural landscape and recreation and eco-tourism services (see Paper I, Table 3 and Paper II, Table 2). Biodiversity, and particularly species richness, were highlighted both by Swedish and Spanish respondents as supporting services at regional level. Primary production services were additionally acknowledged in Spain. Provisioning services were rarely mentioned by Swedish respondents, with timber, fodder and crops being equally named. In contrast Spanish respondents, acknowledged livestock the most, followed by fodder and other services mentioned to much lesser extent. Surprisingly, regulating services were not mentioned by any Swedish respondent at regional level (Figure 5a), whereas Spanish respondents acknowledged climate regulation, water regulation and purification and natural hazard regulation most frequently.

These results are in line with other socio-cultural valuation studies. Livestock was also considered among the most important ES for social well-being among stakeholders, as well as nature recreation activities, rural tourism and environmental education (Oteros-Rozas et al., 2014). This may be a consequence of urban users increasingly demanding environmental education as well as recreational and eco-tourism activities (Martín-López et al., 2012); services which are increasingly being demanded in Europe (Harrison et al., 2010). Grouping stakeholders into different homogeneous categories as done in this study (see Paper I, Table 2; Paper II, Table 1), provides more accurate information on ES demands among different groups of stakeholders (Martín-López et al., 2009b), and therefore might lead to optimal landscape stewardship and land management strategies (Hein et al., 2006). Wood-pastures demonstrate a multi-functional character by delivering multiple ES to stakeholders from different sectors and levels of governance; this stresses the need for further investigation of multiple ES provision in relation to land use change, and to consider the relationship between supply and demand of ES (Wolff et al., 2015). ES important for different stakeholders were not only related to the biological or aesthetic values of the landscape *per se*, nor to its recreational potential alone. Additionally, accessibility of desired benefits in terms of outdoor recreational activities was also highlighted by respondents (Paper I & II), and therefore important to consider for future research and planning (Díaz et al., 2011, Cerqueira et al., 2015).

The presented results demonstrate that the perception of ES by humans is largely context-dependent. When traditional knowledge disappears, the human ability and capacity to perform multi-functional agricultural practices is compromised. At the same time the generation that holds the knowledge to perform multi-functional traditional management practices has not been successful in transmitting this knowledge to younger generations in Sweden. This has two main consequences: an extreme simplification of the management of wood-pastures and, a lack of knowledge and incentives to engage in traditional farming and wood-pasture management. Values and visions of societies are continuously changing, both across time and among individuals, and that might affect the willingness of people to engage in agricultural practices that maintain wood-pastures; other commodities are today more valued. In Spain even when traditional management practices ceased in the 1960s, there are better opportunities for the transmission of traditional ecological knowledge. Additionally, only few people in Sweden depend on the management of wood-pastures for their livelihoods, and thus the recreation function of the landscape is dominant. In Spain, it is common to combine some farming activities with other occupation, and therefore the use of the landscape and the perception of ES is much richer, which reinforces additional identity values. This highlights the importance of cultural ES as key services for people (Plieninger et al., 2015a, Plieninger et al., 2013, Blicharska et al., 2017). Maintaining such key cultural services is thus a milestone in landscape conservation and planning. This new knowledge can also guide more integrative agri-environmental policies deeming to be crucial for a more balanced future (Plieninger et al., 2015b). Additionally, traditional knowledge and practices such as transhumance has been positively related to biodiversity (Hevia et al., 2013), and appeared to be an important factor for holm oak regeneration of *dehesas* (Carmona et al., 2013), and may therefore influence the system maintenance and stability. Thus, cultural ES may play an important role and aid to elucidate current drivers of land use change which may also be fundamental to tackle potential future management issues (Szücs et al., 2015). The abandonment of such traditional practices may however endanger the provision of important services for people and the conservation of wood-pasture landscapes in the long term. To date, cultural ES associated to aesthetical and recreational values of landscapes have already been acknowledged (Daniel et al., 2012). However traditional knowledge, heritage values, cultural landscape, as well as education and knowledge have not been yet targeted, nor included into political commitments. These immaterial dimensions are highly valued services in wood-pastures and should therefore be implemented into specific policies so land managers and ranchers can be financially supported for the supplied services to society (Gaspar et al., 2016). This may potentially be achieved by the creation of specific Payment for Ecosystem Services (PES) integrated into CAP agri-environmental schemes. Additionally, integrative approaches, such as High Nature Value (HNV) farming systems (Oppermann et al., 2012) may become valuable tools to understand the connections of ecosystem functioning and associated ES, as well as the role of the different components of wood-pasture landscapes (Plieninger et al., 2015b, Sohel et al., 2015). In Swedish and Iberian wood-pastures, the provision of ES is the result of traditional land use practices as a necessary condition for the delivery of multiple services as reported in this and previous studies (Bugalho et al., 2011, Huntsinger and Oviedo, 2014).

5.1.2 Challenges for conservation

At European level the importance of wood-pasture has been recognized (Plieninger et al., 2015b, Hartel et al., 2013, Hartel et al., 2015). However, they are still subjected to changing socio-economic processes and are commonly becoming degraded and fragmented (Bergmeier and Roellig, 2014). Current threats such as urban sprawl, land abandonment or agricultural intensification entail even greater uncertainty for the long term conservation of valuable wood-pasture landscapes in Europe (Bergmeier and Roellig, 2014, Moreno and Pulido, 2009, Bugalho et al., 2011, Plieninger et al., 2015b).

Wood-pastures in Sweden are deteriorating due to land abandonment and the absence of livestock (CAB, 2005), active transformation of agricultural land into Norway spruce plantations (Brunet et al., 2012, Paltto et al., 2011) and habitat fragmentation (Öckinger et al., 2012a). Additionally, the beauty of the landscape attracts people to live closer to wood-pastures, which promotes further fragmentation of habitats due to urbanization and grey infrastructure development (Lättman et al., 2014). The restoration of wood-pastures is of limited effect unless grazing is maintained and oak regeneration is secured (Paper II). According to regional officials, two thirds of wood-pasture habitats with high natural values are abandoned and need restoration. However, clearing secondary woodlands and introducing grazing regimes are of marginal profitability today. Additional reported constraints were hard working conditions, lack of financial support and new entrants into farming.

Wood-pastures in Spain are currently threatened by tree regeneration failure (Plieninger et al., 2004), oak diseases (Brasier, 1996), land use change, transformation or abandonment (Bugalho et al., 2011) as well as intensification (Moreno and Pulido, 2009). Spanish respondents were also concerned about hard working conditions and the marginal profitability of their high quality products. They expressed additional concerns about the loss of traditional knowledge, excessive grazing pressure with negative consequences for tree regeneration and wood-pasture stability, the abandonment of traditional practices like transhumance, and climate change. According to respondents this traditional practice (transhumance), which is nowadays mostly abandoned, allowed wood-pastures to recover from the pressure livestock exerted to the system, by taking advantage of foraging resources available elsewhere and providing flexibility and mobility in response to climate variability (Oteros-Rozas et al., 2012). Institutional factors were also commonly mentioned, including the lack of a new specific legal framework for *dehesas*. Today it falls under the forestry legislation, agriculture, livestock and environment, which all hinder an integrated management of wood-pastures. Indeed, due to its multi-functional character, the *dehesa* system is far from being understood by strict mono-sectorial policies (Guzmán Álvarez, 2016). Further, the disappearance of *dehesa* multi-functional practices and products can partially be attributed to the actual low profitability of the generated secondary products like firewood, charcoal, meat, cereals. Ranchers and herders generally stressed the low profitability of farming and ranching, referring to market prices obtained 30-40 years back. They also commented that quality was not prized by the market. High quality extensively produced products had the same market value than intensively produced conventional ones, and thus many ranchers have changed to more productive breeds or mix-breeds. How can then multi-functionality and promotion of the diversity of practices and associated products be fostered? In this regard, recent research has highlighted the most relevant factors in the purchase of food products by consumers (Gaspar et al., 2016). These were price, quality, brand name and origin, and therefore may suggest the development of Protected Designation of Origin (PDO), and their identification with quality brands. Such PDO’s should encompass geographical areas rather than specific products, and be related to specific traditional management practices to ensure the highest quality of the product as well as the diverse and multi-functional sustainable management of farmlands.

5.2 Wood-pasture treatment: experimental ecology (Paper III and IV)

5.2.1 Novel restoration alternatives

Can we find plausible alternatives for wood-pasture restoration and management in Sweden given the identified challenges?

To answer this question the effect of horse browsing on the forest structure and composition was experimentally tested (Paper III). Horse browsing significantly reduced tree height/diameter ratios for European ash (t-test = -6.5, df = 55.4, p-value < 0.01), rowan (t-test = -5.0, df = 92.7, p-value < 0.01), sallow (t-test = -6.5, df = 69.5, p-value < 0.01), blackthorn (t-test = -4.8, df = 110, p-value < 0.01), aspen (t-test = -7.3, df = 331.3, p-value < 0.01), and silver birch (t-test = -5.2, df = 81.9, p-value < 0.01), but not for pine, spruce and oak (Figure 6). This implies that for a given diameter, seedlings and saplings were generally lower at experimental browsed conditions than at controls, and therefore horses can affect the structure of forest understory. The lack of such effect on pine was most probably due to low pine occurrence; for spruce however, only two browsed twigs were recorded and therefore no such relation was found due to herbivore avoidance (Paper III). Studies on oak recruitment have shown that regeneration is prevented by browsing (Kuiters and Slim, 2002, Götmark et al., 2005) although resistance to browsing has also been reported and this in combination to the short study period (three years), might explain the present results despite the high browsing pressure reported here (Table 1). Additionally, the total number of seedlings and saplings were also significantly lower in experimental conditions compared to controls (t-test; t = -12.22, df = 1057.4, p < 0.01). Seedling density has also been reported to decrease as deer density increase (Gill and Morgan, 2010); pattern commonly observed in previous investigations (Gill, 1992a, Gill, 1992b, Gill, 2006, Ward et al., 2008). Reductions of the understory structural complexity has also been described in relation to high deer numbers (Corney et al., 2008, Martin et al., 2010), as well as altered tree size distributions (Peltzer et al., 2014).

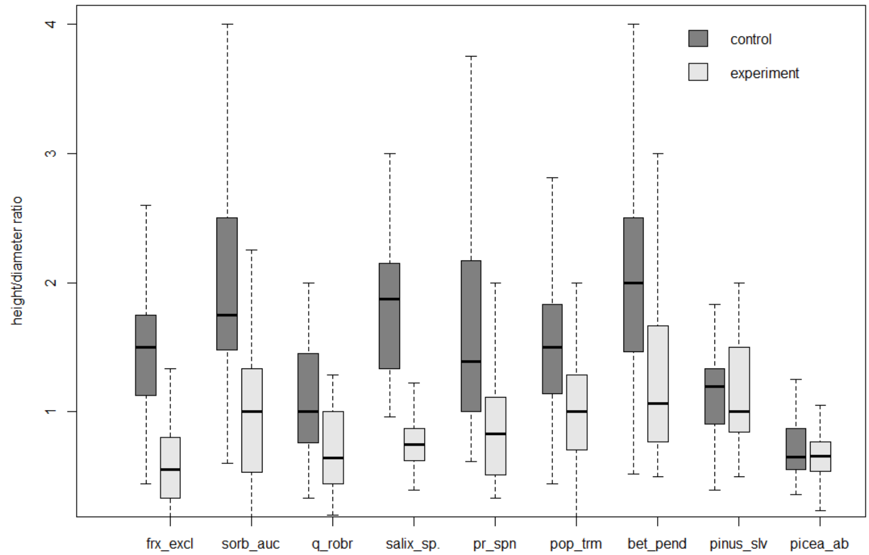


Figure 6. Height/diameter ratio for trees in experimental and control plots. This ratio was utilized as proxy to elucidate the effect of browsing on forest structure. Outliers are not shown to enhance boxplot visibility.

The magnitude of the effect however, may be modulated by the preference of deer for certain tree species (Månsson et al., 2007), the relative forage quality (Pollock et al., 2005) and availability (Hörnberg, 2001, Bergqvist et al., 2014), plant resistance mechanism to herbivory (Gill, 2006), and previous history of browsing (Palmer and Truscott, 2003). In this experiment, the browsing pressure, tree consumption and selection for horses was assessed, as potential tool for the restoration and maintenance of wood-pastures; assessment not tested before. The rustic characteristics of the horse breed in combination with the feral conditions and absence of supplementary feeding in which they were experimentally kept, resembles the impact of wild horses in ecosystems and make their effects comparable with other sympatric wild herbivores. Paper III describes how browsing pressure decreased from ash to, rowan, oak, sallow, blackthorn, aspen, silver birch, and scots pine in relation to availability, ranging from 71% of browsed twigs in ash to 19% for pine. This resulted in a four times higher probability for ash of being browsed compared to pine (Table 1). Similar results were reported for moose by Månsson et al. (2007) although moose exerted a much higher selectivity for preferred tree species. A consequence of a sustained browsing pressure on preferred tree species can lead to plant compositional changes and the dominance of browse resistant species (Gill, 1992a, Gill and Beardall, 2001, Gill, 2006, Côté et al., 2004, White, 2012, Holm et al., 2013). For instance, Tilghman (1989) reported studying white-tailed deer (*Odocoileus virginianus*) a clear decline of browse-sensitive species and diversity with increasing deer density. More recently, decades of sustained browsing pressure have been shown to severely limit the development of palatable species and shift the dominance towards non-preferred species such as *Picea glauca* in North America (White, 2012). In Japan, sika deer (*Cervus nippon*) browsing has altered the forest structure and composition by favoring unpalatable shade-intolerant plant species (Takatsuki, 2009).

Table 1. *Mean values ± SD for tree species availability and browsing pressure estimates. Consumption, selectivity parameters and tree relative preference estimates are also shown*

	Ash	Rowan	Oak	Sallow	Blackthorn	Aspen	Birch	Pine
Tree species availability [a]	0.11 ±0.12	0.13 ±0.07	0.11 ±0.11	0.08 ±0.10	0.13 ±0.13	0.31 ±0.17	0.10 ±0.08	0.02 ±0.04
Browsing pressure [b]	0.71 ±0.10	0.55 ±0.12	0.53 ±0.11	0.47 ±0.13	0.36 ±0.14	0.35 ±0.14	0.27 ±0.13	0.19 ±0.11
Consumption [c]	0.08 ±0.02	0.07 ±0.02	0.06 ±0.02	0.04 ±0.03	0.05 ±0.04	0.11 ±0.05	0.03 ±0.02	0.004 ±0.010
Selectivity parameter [d]	0.21	0.16	0.15	0.14	0.10	0.10	0.08	0.05
Relative preference [e]	3.73	2.89	2.79	2.49	1.89	1.86	1.40	****

Note: [a] Tree species (forage) availability was estimated as the number of focal tree species divided by the total number of species recorded in experimental plots. Species with low occurrences and Norway spruce were excluded from the calculations. [b] Browsing pressure was obtained as the ratio between the number of browsed twigs divided by the total number of twigs up to three meters per selected tree species. [c] Consumption was computed as the product of the previous two values. [d] The selectivity parameter per tree species was calculated based on eq. 2 (see section 4.4.1. Statistical analysis). [e] The relative preference index was computed utilizing eq. 3 and using Scots pine as reference species, i.e., the denominator in eq. 3. **** represents the reference species.

The results provide empirical evidence on the effects of horse browsing on forest structure and composition, and therefore suggest their potential use for wood-pasture restoration and management in south-central Sweden. This, combined with quantitative browsing and tree consumption estimates, as well as quantitative estimates of tree species selectivity, i.e., the probability of a tree species of being browsed in relation to the species availability, create a management "tool-kit" that may facilitate evidence-based biodiversity conservation oriented management efforts for abandoned wood-pasture habitats.

5.2.2 Testing for biodiversity conservation

Is the introduction of a large herbivore supporting grassland biodiversity?
To answer this question the effect of horse grazing on the functional composition of grasslands communities and effects on plant species richness was investigated. Additionally, the effect on pollinator species richness was also tested.

At the community level, the functional composition of the grassland vegetation gradually changed in response to grazing (Paper IV, Figure 3 and 4). Grazing favored prostrate plant species with high specific leaf area (GLMM, $\beta \pm SE$; -0.17 ± 0.08, p-value = 0.04), and lower plant height at maturity (GLMM, $\beta \pm SE$; -0.31 ± 0.13, p-value = 0.02), characteristic of ruderal (GLMM, $\beta \pm SE$; 0.03 ± 0.01, p-value < 0.01) communities. This change occurred rapidly (Figure 7). The same pattern has also been observed for sheep grazing in Patagonian steppe grasslands (Cingolani et al., 2005). The abandonment of grazing regimes, on the other hand, may favor competitive and taller species (Paper IV) which have advantages when competing for light (Grime, 1977), whereas shorter plants can maximize growth by reducing costs related to structural support (Westoby et al., 2002). This response of the grassland community can be interpreted as exerting a mixed tolerance-avoidance response to grazing. For example, plant height and SLA are functional traits intimately related to plant growth, photosynthetic capacity and leaf turnover rate, considered important trade-offs between growth and anti-herbivore defense (Westoby et al., 2002, Reich et al., 2007). Higher SLA values are associated to rapid growth under intense grazing conditions; and thus representing a grazing-tolerance strategy of plants to grazing (Laliberte et al., 2012), and favouring faster growing more palatable plants (Westoby et al., 1999). Shorter plant height, however, has been associated to herbivory resistance as mechanism of grazing avoidance which corroborates the present results (Díaz et al., 2001, Cingolani et al., 2005, Zheng et al., 2015).

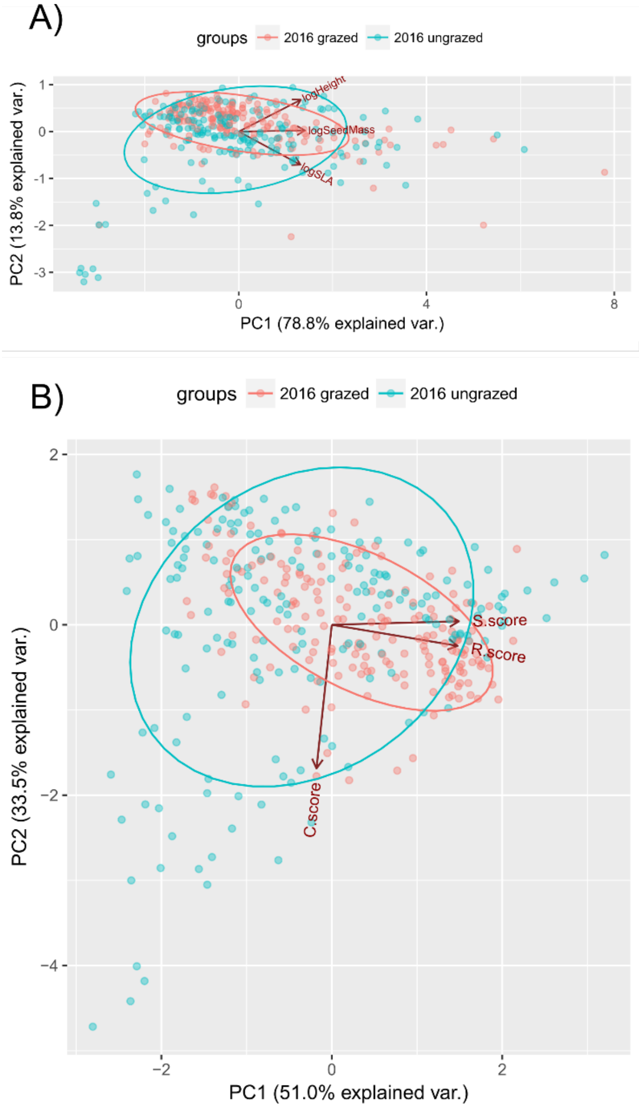


Figure 7. PCA applied to Westoby's LHS (A) and Grime's CSR (B) community weighted mean (CWM) functional traits to illustrate the change in the grassland plant community after three years of treatment. X axes represent the first principal component, while Y axes correspond to the second principal component. In parenthesis the explained variation of each component is presented.

Shorter vegetation, such as in the grazed plots, are expected to favour higher species richness as grazing may impede competitive species to dominate the vegetation community (Pykälä et al., 2005). Accordingly, a significant interacting effect of higher plant species richness was detected in grazed compared to ungrazed areas and time. Further, this difference in plant species richness increased with time (Figure 8; see Paper IV, Table 1).

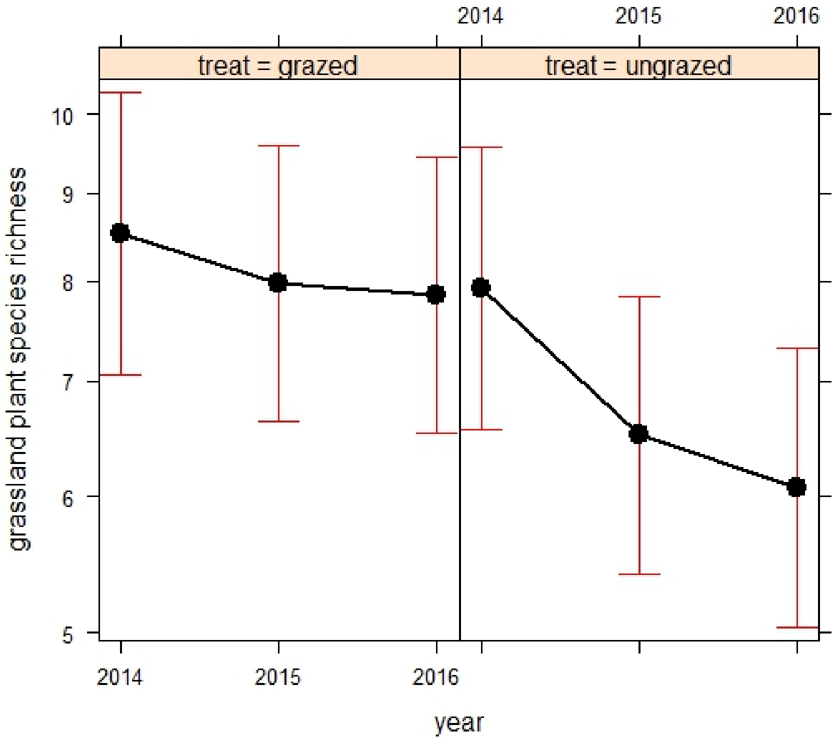


Figure 8. Interaction effect of plant species richness in relation to time and treatment (grazed vs. ungrazed). Shown interacting effects are significant.

In Europe, positive effects of grazing on plant species richness have been shown for cattle (Pykälä, 2003, Pykälä, 2005, Pöyry et al., 2004), sheep (Hellström et al., 2003), and cattle and horse grazing compared to sheep (Öckinger et al., 2006), whereas negative effects of sheep grazing have also been reported (Krahulec et al., 2001). Positive effects of grazing have also been observed in North America for cattle (Beck et al., 2015) and bison (*Bison bison*) (Knapp et al., 1999). Positive effects may depend on herbivore assemblages including large herbivores and habitat productivity (Bakker et al., 2006, Lezama et al., 2014). However, the results presented in Paper IV do not explain the general decline of plant species richness with time. In addition, plant species richness has been shown to increase when grazing is re-introduced, and is strongly related to historical land use (Cousins, 2006). Thus additive landscape and land-use effects may potentially explain the general decline of plant species richness with time observed in this study (Tscharntke et al., 2012, Öckinger et al., 2012b).

A higher butterfly species richness was also found in grazed areas (GLMMPQL, $\beta \pm SE$; -2.11 ± 0.85, p-value = 0.04); pattern followed both by generalist (GLMMPQL, $\beta \pm SE$; 0.61 ± 0.16, p-value < 0.01) and specialist butterfly species (GLMMPQL, $\beta \pm SE$; 0.64 ± 0.17, p-value < 0.01). This is however in contrast with the general pattern described for European temperate grasslands, where a higher butterfly species richness is expected in taller and more structurally diverse vegetation (Milberg et al., 2016, Pöyry et al., 2004), however this is much related to grazing intensity and could explain this contradiction. Additionally, low intensity (extensive) grazing can have positive effects on the structural diversity of grassland vegetation by exhibiting spatial selectivity in feeding, defaecation and wallowing (van Klink et al., 2015). Indeed, Zhu et al. (2012) reported that plant structural diversity was the major factor associated to insect diversity on grazed grasslands. Bumble bee species richness was also higher in grazed compared to ungrazed areas (GLMMPQL, $\beta \pm SE$; -0.58 ± 0.16, p-value = 0.01). Short (GLMMPQL, $\beta \pm SE$; 0.61 ± 0.12, p-value < 0.01) and long-tongued bumble bees (GLMMPQL, $\beta \pm SE$; 0.64 ± 0.12, p-value < 0.01) were also higher in grazed areas, suggesting a positive effect of grazing for both generalist and specialist bumble bee species. Different functional groups of bees might differ in their response to habitat loss (Bommarco et al., 2010, Williams et al., 2010), in particular long-tongued bumble bees with narrow diet breadth are especially vulnerable (Bommarco et al., 2011) and therefore more sensitive to habitat loss and intensification or abandonment of agricultural landscapes (Clough et al., 2014). Flower abundance has been shown to positively correlate with bee community composition (Sjödin et al., 2008), and may explain the use of grazed habitats by a higher number of bumble bee species (Paper IV). To conclude, grazing is revealed as a key factor to maintain grassland plant species richness and may thus tackle disproportionate negative effects of landscape abandonment as well as cascading effects on pollinator assemblages and ecosystem services important for the conservation and functioning of grassland ecosystems in agricultural landscapes. Although grazing and browsing by horses have shown to aid wood-pasture restoration and management (Paper III) and have positive effects on plant and insect biodiversity (Paper IV), the full complexity of wood-pasture management and biodiversity conservation depend on additional factors such as fire regimes, a diversity of herbivory assemblages and human management.

5.3 Looking back to see forward and concluding remarks

Stakeholders from Sweden and Spain have shown both similarities and divergences concerning ES perception. Such similarities and differences can be better understood by putting them in the framework of space-place theories of human-landscape interaction (Hunziker et al., 2007). In space theories the landscape is perceived to fulfill human needs, i.e., instrumental value, whereas landscapes in place theory are the arenas for self-reflection and values, norms and meaning providers. Therefore, when humans settle in a certain environment (space), and establish particular links to it in terms of cultural values, personal experiences and social meanings, that environment transforms into a place for them (Tuan, 1977). In Sweden, most valued services were related to landscape beauty and recreation and eco-tourism services (i.e., cultural ES). Feeling and appreciating the beauty of these savannah-like landscapes might be explained by the information (Kaplan and Kaplan, 1989), savannah (Orians, 1980), prospect-refuge (Appleton, 1975) and psycho-evolutionary (Ulrich, 1983) theories. These cultural services arise when landscapes are mainly perceived as spaces, as today wood-pastures are remnant and severely fragmented habitats in Sweden. In contrast, Spanish respondents additionally perceived wood-pastures (*dehesas*) as places, since they live within a wood-pasture matrix, and have therefore created associated values and social identities with the landscape, transforming wood-pastures into places. They therefore additionally highlighted services as sense of place and identity values, traditional knowledge, cultural landscape and heritage values. Indeed, places symbolizing collective belonging, places used during childhood, for recreation and frequented natural areas, have been shown of high significance to local people (Buchecker, 2005, Korpela et al., 2001). Likewise, as the amount of time spent in a place increases, the attachment to that place, i.e., sense of place, increases accordingly (Hay, 1998). The benefits of wood-pastures (Paper I & II) and natural environments on human health and well-being, may also contribute to the perceived high value of wood-pastures reported both in Sweden and Spain, as shown in recent research (Berman et al., 2008, Hartig et al., 2011, Hartig et al., 2014). The results from this thesis pose nevertheless many questions for further research. Given that sense of place can foster landscape conservation (Eisenhauer et al., 2000) and environmental concern (Williams et al., 1992), what would the impact of naturbanization (sensu Velasco, 2008) be on sense of place and identity regulation? Cultural ES were in both Sweden and Spain acknowledged as very important services, but for different reasons. Thus, this differences seem to represent the two poles of the perceptual development of cultural services in increasingly urbanized societies. The former perceiving primarily recreational services from wood-pastures, whereas the latter traditional knowledge and identity values, which are currently being eroded by socio-economic changes. How large a landscape should be to provide important services that trigger landscape and biodiversity conservation and therefore the provision of important services to people?

As societies “develop” and become more and more urbanized, the challenges wood-pastures face change accordingly. In southern Sweden, wood-pastures are vanishing surrounded by other dominant land uses and only surviving in big estates or protected public land refuges. In Spain, the loss of traditional knowledge and practices (multi-functionality) is dually changing and simplifying management practices which compromise wood-pasture stability in the long term by intensification and limit the provision of services co-generated by human-nature interactions (Fischer and Eastwood, 2016, Palomo et al., 2016). Immaterial dimensions and recreational services are highly valued services in wood-pastures, and therefore the creation of specific Payment for Ecosystem Services (PES) integrated into policy could financially support farmers and ranchers for the supplied services to society (Gaspar et al., 2016). To increase the value of wood-pasture landscapes and associate products, the development of Protected Designation of Origin (PDO) brands could also foster valuation of products and services, and thus landscape conservation, given that agricultural practices and products are of marginal profitability today. However, a major challenge is how to promote people to engage in farming and therefore support rural environments and wood-pasture landscape conservation. It is clear that wood-pastures need to be managed in order to retain their structural characteristics through which the expression of biodiversity and ES is supported and delivered. Humanity may currently face paradigm changes in which assets such as biodiversity and ES are hard to translate into monetary terms and thus difficulty to assess. This may consequently pose major challenges in the future to sustain a harmonious living planet if current disproportionate anthropogenic effects are not tackled.

Large herbivores could be re-introduced for wood-pasture restoration and management, and thus facilitate biodiversity conservation oriented management efforts for abandoned wood-pasture and forest habitats. Wood-pastures in Sweden normally occur interspersed with other habitats, which are populated by sympatric wild herbivores whose tree preferences are similar to the ones reported here (Månsson et al., 2007, Angelstam et al., 2017b). Thus the combined effect of sympatric large herbivore communities, including large and megaherbivore fauna, on forest and wood-pasture structure and composition for future restoration and management oriented programs should be therefore further investigated. As recently demonstrated, human impact on trophic interactions between predators, large herbivores and vegetation can affect young deciduous tree recruitment to mature canopy trees (Angelstam et al., 2017a) and therefore hampering the future key-stone functions of such tree species for biodiversity. Continued wood-pasture management in the experimental study conditions may lead to long-term plant compositional changes, shifting from pine-spruce dominated to probably oak-aspen-spruce dominated wood-pastures. Oak, aspen, and spruce are considered foundation species (Ellison et al., 2005) because of the disproportionate impact they exert on community and ecosystem properties in relation to their abundance and could therefore be targeted for biodiversity conservation oriented management. The conservation of such species and wood-pasture structural characteristics does not have to be maintained by agricultural management practices alone. The re-introduction of large mammal herbivores and fire (cease suppression) may generate the desire landscape attributes and support the species of high conservation value in self-regulating ecosystems (Bond, 2005, Svenning et al., 2016).

Biodiversity is subjected to a global decline (Butchart et al., 2010, Barnosky et al., 2011, Ceballos et al., 2015). Current defaunation processes are also affecting other species and ecosystem functioning (Ripple et al., 2014, Ripple et al., 2017, Dirzo et al., 2014), as well as the extinction of ecological interactions (Valiente-Banuet et al., 2015), expected to continue in the future (Pereira et al., 2010). In Europe, the decline of biodiversity is particularly severe in agricultural landscapes controlled either by agricultural intensification or abandonment (Krebs et al., 1999, Landis, 2017, Berendse et al., 2004). Quantitative estimates reported a 28% decline for plant species, 54% for birds, and 71% for butterfly species over the last decades in Britain (Thomas et al., 2004). In addition, a dramatic reduction in flying insect biomass was recently reposted by Hallmann et al. (2017) with expected far reaching consequences on ecosystem functioning. The results from Paper IV show that horse grazing can have rapid positive effects on the functional composition of grassland communities, plant species richness and cascade effects on pollinators. Therefore the re-introduction of large herbivores can have positive effects on biodiversity and ecosystem functioning. However, in order to assess the full potential of horses for biodiversity conservation in Sweden and elsewhere, we should designate large areas to experimentally test the effect of richer herbivore communities, with different stocking rates and habitat productivity gradients and monitor their effect for the restoration and management of forest and species-rich semi-natural grasslands. Wood-pastures and semi-natural grassland are the most species-rich habitats in Sweden (Svensson, 1988), and traditionally grazed grasslands are the most plant species-rich ecosystems in Europe (Wilson et al., 2012). The first two chapters of the thesis highlighted the importance of cultural services to people and their key function for wood-pasture conservation. Wood-pastures are millennial ancient ecosystems, shaped throughout centuries by human activities. The multi-purpose agricultural management practices are not profitable today and this poses serious challenges for wood-pasture conservation in the long term. Former prehistorical ecosystems may have had similar characteristics than wood-pastures today. If so, could the ancestors of extant domesticated mega-herbivores shaped the landscape as modern humans in historical times?

Late Quaternary megafaunal extinctions were not only driven by a dramatic change in climatic conditions but also coincide with human arrivals and therefore anthropogenic combined with climatic factors modulated such extinction patterns (Prescott et al., 2012). Indeed, human-caused extinction of Quaternary megafauna has been recently confirmed (Sandom et al., 2014). Moreover, later *Homo sapiens* global expansion also had dramatic consequences on prehistoric megafauna extinctions (Barnosky et al., 2004, Sandom et al., 2014). This led to a progressive simplification of the megafaunal component of ecosystems, and subsequent cascading effects on plant community composition, vegetation structure, fire regimes (Gill, 2014) as well as ecological interactions (Galetti et al., 2017); pattern that still continues today (Dirzo et al., 2014). This demonstrates that humans have exerted a significant effect on ecosystem change for long time. Hence, which ecosystem state or baseline should we aim for in conservation? A new scientific approach, i.e., trophic rewilding, aiming at restoring trophic cascades to promote self-regulating biodiverse ecosystems (Svenning et al., 2016), may contribute to the development of new narratives and science-based initiatives and thus to help palliate current unprecedented global challenges and biodiversity declines. Current and former megaherbivore fauna (≥ 1000 kg) have a disproportionate effect on ecosystems (Owen-Smith, 1987) due to their abundance and ecosystem engineering effects (Haynes, 2012), and were not top-down regulated by predators (Van Valkenburgh et al., 2016). Similarly, large herbivores in some ecosystems are neither regulated by predators rather largely bottom-up regulated (Hopcraft et al., 2010). Additionally due to their ecological importance, the disappearance of megafauna have produced ecological state shifts in different biomes (Barnosky et al., 2016). Consequently, ecological state shifts have likely occurred in Europe as well, affecting the composition and structure of vegetation and ecosystem function. Therefore, re-introducing extinct large herbivore taxa with equivalent ecologically functional substitutes could mitigate global biodiversity declines and foster self-regulating ecosystems. Potential candidates for Europe could be European bison (*Bison bonasus*), and rustic cattle and horse breeds. It seems plausible that herbivore assemblages including substitutes of recently extinct large and megaherbivores may tackle biodiversity declines and re-structure and re-shape ecosystems to prehistoric analogues. Appropriating terrestrial surface for rewilding, in response to agricultural land abandonment in Europe, will likely generate additional human-wildlife conflicts to account for, and may reduce the provision of some services (e.g., food) but possibly foster others especially regulating and cultural services (Cerqueira et al., 2015). Such actions may mitigate the ubiquitous biodiversity decline and accelerated defaunation processes, but not completely halter planetary biodiversity loss (Crutzen, 2002). Wilson (2000) argue that we need to save as much as 50% of terrestrial ecosystems for biodiversity and planetary balance. Will that suffice to tackle current biodiversity declines? Human impacts have tremendously escalated at global scale for the last three hundred years and therefore the Anthropocene as new geological era has been suggested (Crutzen, 2002). Does current research really contributing to a global environmental amelioration? Is there a way to sustain the planetary biodiversity and life sustaining systems without changing the human approach to nature and natural environments? This thesis show that cultural services and biodiversity are key services to people, and that the re-introduction of extant domesticated large herbivores may benefit wood-pasture restoration and management, while supporting pollinators and ecosystem functioning. Most probably sense of place and attachment values would favor the conservation of wood-pastures by humans, while already abandoned (or highly degraded) areas perceived today as spaces, could potentially host rewilding experiences. That may lead to a plausible change in narratives and culminate in the development of different human-nature interactions that ultimately will convert such spaces back into wilder places. Large areas in Sweden and Spain are suitable for rewilding (Cerqueira et al., 2015). However, modern lifestyle, industrialization, and urbanization are dually harmful for nature and humanity, as long known and expressed in the following quote:

> "The tendency nowadays to wander in wildernesses is delightful to see. Thousands of tired, nerve-shaken, over-civilized people are beginning to find out that going to the mountains is going home; that wildness is a necessity; and that mountain parks and reservations are useful not only as fountains of timber and irrigating rivers, but as fountains of life. Awakening from the stupefying effects of the vice of over-industry and the deadly apathy of luxury, they are trying as best they can to mix and enrich their own little ongoings with those of nature, and to get rid of rust and disease" (Muir, 1901).

Are we ready to go a step forward for conservation? *Alia iacta est*

References

AHTI, T., HÄMET-AHTI, L. & JALAS, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici***,** 169-211.

AITCHISON, J. 1986. *The statistical analysis of compositional data,* Ney York, Chapman and Hall.

ALANEN, E. L., HYVÖNEN, T., LINDGREN, S., HÄRMÄ, O. & KUUSSAARI, M. 2011. Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside. *Journal of Applied Ecology,* 48**,** 1251-1259.

ANGELSTAM, P., MANTON, M., PEDERSEN, S. & ELBAKIDZE, M. 2017a. Disrupted trophic interactions affect recruitment of boreal deciduous and coniferous trees in northern Europe. *Ecological Applications,* 27**,** 1108-1123.

ANGELSTAM, P., PEDERSEN, S., MANTON, M., GARRIDO, P., NAUMOV, V. & ELBAKIDZE, M. 2017b. Green infrastructure maintenance is more than land cover: Large herbivores limit recruitment of key-stone tree species in Sweden. *Landscape and Urban Planning,* 167**,** 368-377.

APPLETON, J. 1975. *The experience of landscape,* New York, Wiley.

ASLAN, C. E., ZAVALETA, E. S., TERSHY, B. & CROLL, D. 2013. Mutualism disruption threatens global plant biodiversity: a systematic review. *PLoS One,* 8**,** e66993.

ATKINSON, R. & FLINT, J. 2004. *Snowball Sampling. The SAGE Encyclopedia of Social Science Research Methods.,* Thousand Oaks, CA, SAGE Publications, Inc.

BAKKER, E. S., RITCHIE, M. E., OLFF, H., MILCHUNAS, D. G. & KNOPS, J. M. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology letters,* 9**,** 780-788.

BAN, N. C., MILLS, M., TAM, J., HICKS, C. C., KLAIN, S., STOECKL, N., BOTTRILL, M. C., LEVINE, J., PRESSEY, R. L., SATTERFIELD, T. & CHAN, K. M. A. 2013. A social–ecological approach to conservation planning: embedding social considerations. *Frontiers in Ecology and the Environment,* 11**,** 194-202.

BARNOSKY, A. D., KOCH, P. L., FERANEC, R. S., WING, S. L. & SHABEL, A. B. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *science,* 306**,** 70-75.

BARNOSKY, A. D., LINDSEY, E. L., VILLAVICENCIO, N. A., BOSTELMANN, E., HADLY, E. A., WANKET, J. & MARSHALL, C. R. 2016. Variable impact of late-

Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proceedings of the National Academy of Sciences,* 113**,** 856-861.

BARNOSKY, A. D., MATZKE, N., TOMIYA, S., WOGAN, G. O., SWARTZ, B., QUENTAL, T. B., MARSHALL, C., MCGUIRE, J. L., LINDSEY, E. L. & MAGUIRE, K. C. 2011. Has the Earth's sixth mass extinction already arrived? *Nature,* 471**,** 51-57.

BECK, J. J., HERNÁNDEZ, D. L., PASARI, J. R. & ZAVALETA, E. S. 2015. Grazing maintains native plant diversity and promotes community stability in an annual grassland. *Ecological Applications,* 25**,** 1259-1270.

BERENDSE, F., CHAMBERLAIN, D., KLEIJN, D. & SCHEKKERMAN, H. 2004. Declining biodiversity in agricultural landscapes and the effectiveness of agri-environment schemes. *Ambio,* 33**,** 499-502.

BERGMAN, K.-O., ASK, L., ASKLING, J., IGNELL, H., WAHLMAN, H. & MILBERG, P. 2007. Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors. *Biodiversity and Conservation,* 17**,** 139-153.

BERGMAN, K.-O., ASKLING, J., EKBERG, O., IGNELL, H., WAHLMAN, H. & MILBERG, P. 2004. Landscape effect on butterfly assemblages in an agricultural region. *ECOGRAPHY,* 27**,** 619-628.

BERGMEIER, E., PETERMANN, J. & SCHRÖDER, E. 2010. Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. *Biodiversity and Conservation,* 19**,** 2995-3014.

BERGMEIER, E. & ROELLIG, M. 2014. Diversity, threats and conservation of European wood-pastures. *In:* PLIENINGER, T. H. A. T. (ed.) *European Wood-pastures in Transition. A social-ecological approach.* Oxon and New York: Routledge.

BERGQVIST, G., BERGSTRÖM, R. & WALLGREN, M. 2014. Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests–effects of forage availability, moose population density and site productivity. *Silva Fennica,* 48**,** 1-13.

BERGSTRÖM, R., JERNELID, H., LAVSUND, S., LUNDBERG, P. & WALLIN, K. 1995. Älgtäthet-betestryck-fodertillgång-skogstillstånd-skadenivåer-skaderisker [Moose density-browsing pressure-forage availability-forest composition-forest damage-damage risks]. Projekt Balanserad älgstam, Final report. Swedish Hunters' Association and Swedish University of Agricultural Sciences (SLU).

BERMAN, M. G., JONIDES, J. & KAPLAN, S. 2008. The Cognitive Benefits of Interacting With Nature. *Psychological Science,* 19**,** 1207-1212.

BIESMEIJER, J. C., ROBERTS, S. P., REEMER, M., OHLEMÜLLER, R., EDWARDS, M., PEETERS, T., SCHAFFERS, A., POTTS, S. G., KLEUKERS, R. & THOMAS, C. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science,* 313**,** 351-354.

BLICHARSKA, M., SMITHERS, R. J., HEDBLOM, M., HEDENÅS, H., MIKUSIŃSKI, G., PEDERSEN, E., SANDSTRÖM, P. & SVENSSON, J. 2017. Shades of grey challenge practical application of the cultural ecosystem services concept. *Ecosystem Services,* 23**,** 55-70.

BOGGS, C. L., WATT, W. B. & EHRLICH, P. R. 2003. *Butterflies: Ecology and evolution taking flight,* Chicago, The University of Chicago Press.

BOLKER, B. M., BROOKS, M. E., CLARK, C. J., GEANGE, S. W., POULSEN, J. R., STEVENS, M. H. H. & WHITE, J.-S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution,* 24**,** 127-135.

BOMMARCO, R., BIESMEIJER, J. C., MEYER, B., POTTS, S. G., PÖYRY, J., ROBERTS, S. P., STEFFAN-DEWENTER, I. & ÖCKINGER, E. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society of London B: Biological Sciences***,** rspb20092221.

BOMMARCO, R., LUNDIN, O., SMITH, H. G. & RUNDLÖF, M. 2011. Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences*.

BOND, W. J. 2005. Large parts of the world are brown or black: a different view on the 'Green World'hypothesis. *Journal of Vegetation Science,* 16**,** 261-266.

BRAAT, L. C. & DE GROOT, R. 2012. The ecosystem services agenda:bridging the worlds of natural science and economics, conservation and development, and public and private policy. *Ecosystem Services,* 1**,** 4-15.

BRASIER, C. 1996. Phytophthora cinnamomi and oak decline in southern Europe. Environmental constraints including climate change. *Ann. For. Sci.,* 53**,** 347-358.

BRESLOW, N. E. & CLAYTON, D. G. 1993. Approximate inference in generalized linear mixed models. *Journal of the American statistical Association,* 88**,** 9-25.

BRUNET, J., FELTON, A. & LINDBLADH, M. 2012. From wooded pasture to timber production–changes in a European beech (Fagus sylvatica) forest landscape between 1840 and 2010. *Scandinavian journal of forest research,* 27**,** 245-254.

BUCHECKER, M. 2005. Public place as a resource of social interaction. *In:* TURNER, P. & DAVENPORT, E. (eds.) *Space, spatiality and technology.* Dordrecht: Kluwer.

BUGALHO, M. N., CALDEIRA, M. C., PEREIRA, J. S., ARONSON, J. & PAUSAS, J. G. 2011. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. *Frontiers in Ecology and the Environment,* 9**,** 278-286.

BUTCHART, S. H., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J. P., ALMOND, R. E., BAILLIE, J. E., BOMHARD, B., BROWN, C. & BRUNO, J. 2010. Global biodiversity: indicators of recent declines. *Science,* 328**,** 1164-1168.

CAB 2005. Multi-purpose management of oak habitats. Examples of best practice from the county of Östergötland, Sweden. County administration of Östergötland, report 2005:16.

CADOTTE, M. W., CARSCADDEN, K. & MIROTCHNICK, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of applied ecology,* 48**,** 1079-1087.

CAMPOS, P. 2004. Towards a sustainable global economics approach for Mediterranean agroforestry systems. *In:* SCHNABEL, S. & FERREIRA, A. (eds.) *Sustainability of agrosilvopastoral systems.* Catena Verlag, Reiskirchen, Germany.

CARDINALE, B. J. 2012. Biodiversity loss and its impact on humanity. *Nature,* 486**,** 59-67.

CARMONA, C. P., AZCÁRATE, F. M., OTEROS-ROZAS, E., GONZÁLEZ, J. A. & PECO, B. 2013. Assessing the effects of seasonal grazing on holm oak regeneration: Implications for the conservation of Mediterranean dehesas. *Biological Conservation,* 159**,** 240-247.

CARO, T. 2010. *Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species,* Island Press.

CARVALHEIRO, L. G., KUNIN, W. E., KEIL, P., AGUIRRE-GUTIÉRREZ, J., ELLIS, W. N., FOX, R., GROOM, Q., HENNEKENS, S., LANDUYT, W. & MAES, D. 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters,* 16**,** 870-878.

CEBALLOS, G., EHRLICH, P. R., BARNOSKY, A. D., GARCÍA, A., PRINGLE, R. M. & PALMER, T. M. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science advances,* 1**,** e1400253.

CEDERBERG, B. & MOSSBERG, B. 2012. *Humlor i Sverige,* Stockholm, Bonniers.

CERQUEIRA, Y., NAVARRO, L. M., MAES, J., MARTA-PEDROSO, C., HONRADO, J. P. & PEREIRA, H. M. 2015. Ecosystem services: the opportunities of rewilding in Europe. *Rewilding European Landscapes.* Springer.

CHAN, K. M. A., GUERRY, A. D., BALVANERA, P., KLAIN, S., SATTERFIELD, T., BASURTO, X., BOSTROM, A., CHUENPAGDEE, R., GOULD, R., HALPERN, B. S., HANNAHS, N., LEVINE, J., NORTON, B., RUCKELSHAUS, M., RUSSELL, R., TAM, J. & WOODSIDE, U. 2012a. Where are Cultural and Social in Ecosystem Services? A Framework for Constructive Engagement. *BioScience* 62**,** 744-756.

CHAN, K. M. A., SATTERFIELD, T. & GOLDSTEIN, J. 2012b. Rethinking ecosystem services to better address and navigate cultural values. *Ecological Economics,* 74**,** 8-18.

CHAPIN III, F. S., ZAVALETA, E. S., EVINER, V. T. & NAYLOR, R. L. 2000. Consequences of changing biodiversity. *Nature,* 405**,** 234.

CHESSON, J. 1978. Measuring preference in selective predation. *Ecology,* 59**,** 211-215.

CINGOLANI, A. M., POSSE, G. & COLLANTES, M. B. 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology,* 42**,** 50-59.

CLOUGH, Y., EKROOS, J., BÁLDI, A., BATÁRY, P., BOMMARCO, R., GROSS, N., HOLZSCHUH, A., HOPFENMÜLLER, S., KNOP, E. & KUUSSAARI, M. 2014. Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology letters,* 17**,** 1168-1177.

CORNEY, P., KIRBY, K., LE DUC, M., SMART, S., MCALLISTER, H. & MARRS, R. 2008. Changes in the field-layer of Wytham Woods–assessment of the impacts of a range of environmental factors controlling change. *Journal of Vegetation Science,* 19**,** 287-298.

CORNVALL, E. 2017. Fältinstruktion för fjärilar och humlor i ängs- och betesmarker 2017 [Instructions for monitoring butterflies and bumble bees in pasturelands]. Umeå: Institutionen för skoglig resurshushållning.

COSTA, A., MADEIRA, M., SANTOS, J. L. & PLIENINGER, T. 2014. Recent dynamics of evergreen oak wood-pastures in south-western Iberia. *In:* HARTEL, T. & PLIENINGER, T. (eds.) *European wood pasturess in transition. A social-ecological approach.*

CÔTÉ, S. D., ROONEY, T. P., TREMBLAY, J.-P., DUSSAULT, C. & WALLER, D. M. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.*, 35**,** 113-47.

COUSINS, S. A. O. 2006. Plant species richness in midfield islets and road verges – The effect of landscape fragmentation. *Biological Conservation,* 127**,** 500-509.

CRUTZEN, P. J. 2002. Geology of mankind. *Nature,* 415**,** 23-23.

DAILY, G. C. 1997. *Nature's Services: Societal Dependence on Natural Ecosystems,* Washington DC, Island Press.

DANIEL, T. C., MUHAR, A., ARNBERGER, A., AZNAR, O., BOYD, J. W., CHAN, K. M., COSTANZA, R., ELMQVIST, T., FLINT, C. G., GOBSTER, P. H., GRET-REGAMEY, A., LAVE, R., MUHAR, S., PENKER, M., RIBE, R. G., SCHAUPPENLEHNER, T., SIKOR, T., SOLOVIY, I., SPIERENBURG, M., TACZANOWSKA, K., TAM, J. & VON DER DUNK, A. 2012. Contributions of cultural services to the ecosystem services agenda. *Proc Natl Acad Sci U S A,* 109**,** 8812-9.

DAVIES, A. L. & WATSON, F. 2007. Understanding the changing value of natural resources: an integrated palaeoecological–historical investigation into grazing–woodland interactions by Loch Awe, Western Highlands of Scotland. *Journal of biogeography,* 34**,** 1777-1791.

DE BELLO, F., LAVOREL, S., DÍAZ, S., HARRINGTON, R., CORNELISSEN, J. H., BARDGETT, R. D., BERG, M. P., CIPRIOTTI, P., FELD, C. K. & HERING, D. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation,* 19**,** 2873-2893.

DE BELLO, F., LEPŠ, J. & SEBASTÁ, M.-T. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology,* 42**,** 824-833.

DE GROOT, R., FISHER, B., CHRISTIE, M., ARONSON, J., BRAAT, L., HAINES-YOUNG, R., GOWDY, J., MALTBY, E., NEUVILLE, A., POLASKY, S., PORTELA, R., RING, I., BLIGNAUT, J., BRONDIZIO, E., COSTANZA, R., JAX, K., KADEKODI, G. K., MAY, P. H. & SHMELEV, S. 2010a. Integrating the ecological and economic dimensions in biodiversity and ecosystem service valuation. *In:* KUMAR, P. (ed.) *The Economics of Ecosystems and Biodiversity (TEEB): Ecological and Economic Foundations.* London: Earthscan.

DE GROOT, R. S., ALKEMADE, R., BRAAT, L., HEIN, L. & WILLEMEN, L. 2010b. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecological Complexity,* 7**,** 260-272.

DENZIN, N. K. & LINCOLN, Y. S. 2011. *The SAGE Handbook of Qualitative Research,* London, Sage.

DíAZ, M., CAMPOS, P. & PULIDO, F. J. 1997. The Spanish dehesa: a diversity in land use and wildlife. *In:* PAIN, D. J. & PIENKOWSKI, M. W. (eds.) *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation.* London: Academic Press.

DIAZ, M., TIETJE, W. D. & BARRET, R. H. 2013. Effects of management in biological diversity and endangered species. *In:* CAMPO, P., HUNTSINGER, L., OVIEDO, J. L. & STARRS, P. F. (eds.) *Mediterranean Oak Woodland Working Landscapes: Dehesas of Spain and Ranchlands of California.* New York: Springer.

DÍAZ, S., LAVOREL, S., DE BELLO, F., QUÉTIER, F., GRIGULIS, K. & ROBSON, T. M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences,* 104**,** 20684-20689.

DÍAZ, S., NOY-MEIR, I. & CABIDO, M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology,* 38**,** 497-508.

DÍAZ, S., QUÉTIER, F., CÁCERES, D. M., TRAINOR, S. F., PÉREZ-HARGUINDEGUY, N., BRET-HARTE, M. S., FINEGAN, B., PEÑA-CLAROS, M. & POORTER, L. 2011. Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. *Proceedings of the National Academy of Sciences,* 108**,** 895-902.

DIRZO, R., YOUNG, H. S., GALETTI, M., CEBALLOS, G., ISAAC, N. J. & COLLEN, B. 2014. Defaunation in the Anthropocene. *science,* 345**,** 401-406.

EHRLICH, P. R. & EHRLICH, A. H. 1981. *Extinction: the causes and consequences of the disappearance of species,* London, Gollancz.

EISENHAUER, B. W., KRANNICH, R. S. & BLAHNA, D. J. 2000. Attachments to special places on public lands: An analysis of activities, reason for attachments, and community connections. *Society & Natural Resources,* 13**,** 421-441.

ELIASSON, P. & NILSSON, S. G. 2002. 'You should hate young oaks and young noblemen': the environmental history of oaks in eighteenth-and nineteenth-century Sweden. *Environmental history,* 7**,** 659-677.

ELLISON, A. M., BANK, M. S., CLINTON, B. D., COLBURN, E. A., ELLIOTT, K., FORD, C. R., FOSTER, D. R., KLOEPPEL, B. D., KNOEPP, J. D., LOVETT, G. M., MOHAN, J., ORWIG, D. A., RODENHOUSE, N. L., SOBCZAK, W. V., STINSON, K. A., STONE, J. K., SWAN, C. M., THOMPSON, J., VON HOLLE, B. & WEBSTER, J. R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment,* 3**,** 479-486.

ELMQVIST, T., FOLKE, C., NYSTRÖM, M., PETERSON, G., BENGTSSON, J., WALKER, B. & NORBERG, J. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment,* 1**,** 488-494.

EWERS, R. M. & DIDHAM, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological reviews,* 81**,** 117-142.

EZQUERRA BOTICARIO, F. J. & GIL SANCHEZ, L. 2008. *La transformación histórica del paisaje forestal en Extremadura. Tercer Inventario Forestal Nacional 1997-2007,* Madrid, Ministerio de Medio Ambiente.

FAGERHOLM, N., TORRALBA, M., BURGESS, P. J. & PLIENINGER, T. 2016. A systematic map of ecosystem services assessments around European agroforestry. *Ecological Indicators,* 62**,** 47-65.

FISCHER, A. & EASTWOOD, A. 2016. Coproduction of ecosystem services as human–nature interactions—An analytical framework. *Land Use Policy,* 52**,** 41-50.

FISCHER, J., HARTEL, T. & KUEMMERLE, T. 2012. Conservation policy in traditional farming landscapes. *Conservation Letters,* 5**,** 167-175.

FLYVBJERG, B. 2011. Case Study. *In:* DENZIN, N. K. & LINCOLN, Y. S. (eds.) *The Sage Handbook of Qualitative Research.* Thousand Oaks, CA: Sage.

FOLEY, J. A., DEFRIES, R., ASNER, G. P., BARFORD, C., BONAN, G., CARPENTER, S. R., CHAPIN, F. S., COE, M. T., DAILY, G. C. & GIBBS, H. K. 2005. Global consequences of land use. *science,* 309**,** 570-574.

GALETTI, M., MOLEÓN, M., JORDANO, P., PIRES, M. M., GUIMARÃES, P. R., PAPE, T., NICHOLS, E., HANSEN, D., OLESEN, J. M., MUNK, M., DE MATTOS, J. S., SCHWEIGER, A. H., OWEN-SMITH, N., JOHNSON, C. N., MARQUIS, R. J. &

SVENNING, J.-C. 2017. Ecological and evolutionary legacy of megafauna extinctions. *Biological Reviews***,** n/a-n/a.
GARNIER, E., CORTEZ, J., BILLÈS, G., NAVAS, M.-L., ROUMET, C., DEBUSSCHE, M., LAURENT, G., BLANCHARD, A., AUBRY, D., BELLMANN, A., NEILL, C. & TOUSSAINT, J.-P. 2004. Plant functional markers capture ecosystem properties during secundary succession. *Ecology,* 85**,** 2630-2637.
GARRIDO, P. 2014. *Cultural oak landscapes as green infrastructure for human well-being.* Licentiate Thesis, Swedish University of Agricultural Sciences.
GARRIDO, P., ELBAKIDZE, M. & ANGELSTAM, P. 2017a. Stakeholders' perceptions on ecosystem services in Östergötland's (Sweden) threatened oak wood-pasture landscapes. *Landscape and Urban Planning,* 158**,** 96-104.
GARRIDO, P., ELBAKIDZE, M., ANGELSTAM, P., PLIENINGER, T., PULIDO, F. & MORENO, G. 2017b. Stakeholder perspectives of wood-pasture ecosystem services: A case study from Iberian dehesas. *Land Use Policy,* 60**,** 324-333.
GASPAR, P., ESCRIBANO, M. & MESIAS, F. J. 2016. A qualitative approach to study social perceptions and public policies in dehesa agroforestry systems. *Land Use Policy,* 58**,** 427-436.
GILL, J. L. 2014. Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytologist,* 201**,** 1163-1169.
GILL, R. M. A. 1992a. A Review of Damage by Mammals in North Temperate Forests: 1. Deer. *Forestry: An International Journal of Forest Research,* 65**,** 145-169.
GILL, R. M. A. 1992b. A Review of Damage by Mammals in North Temperate Forests: 3. Impact on Trees and Forests. *Forestry: An International Journal of Forest Research,* 65**,** 363-388.
GILL, R. M. A. 2006. The influence of large herbivores on tree recruitment and forest dynamics. *In:* DANELL, K., BERGSTRÖM, R., DUNCAN, P. & PASTOR, J. (eds.) *Large Herbivore Ecology, Ecosystem Dynamics and Conservation.* New York: Cambridge University Press.
GILL, R. M. A. & BEARDALL, V. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry,* 74**,** 209-218.
GILL, R. M. A. & MORGAN, G. 2010. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry: An International Journal of Forest Research,* 83**,** 53-63.
GÓMEZ-BAGGETHUN, E., DE GROOT, R., LOMAS, P. L. & MONTES, C. 2010 The history of ecosystem services in economic theory and practice: from early notions to markets and payment schemes. *Ecological Economics,* 69**,** 1209-1218.
GOULSON, D. 2003. *Bumblebees: their behavior and ecology,* Oxford, Oxford University Press.
GOULSON, D., HANLEY, M. E., DARVILL, B., ELLIS, J. & KNIGHT, M. E. 2005. Causes of rarity in bumblebees. *Biological conservation,* 122**,** 1-8.
GREENWOOD, J. J. & ELTON, R. A. 1979. Analysing experiments on frequency-dependent selection by predators. *The Journal of Animal Ecology***,** 721-737.
GRIME, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist,* 111**,** 1169-1194.
GRIME, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology,* 86**,** 902-910.

GRIME, J. P., FRIDLEY, J. D., ASKEW, A. P., THOMPSON, K., HODGSON, J. G. & BENNETT, C. R. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences,* 105**,** 10028-10032.

GROVE, A. T. & RACKHAM, O. 2003. *The Nature of Mediterranean Europe. An Ecological History,* New Haven and London, Tale University Press.

GUZMÁN ÁLVAREZ, J. R. 2016. The image of a tamed landscape: dehesa through History in Spain. *Culture & History Digital Journal,* 5**,** e003.

GÖTMARK, F., BERGLUND, Å. & WIKLANDER, K. 2005. Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. *Scandinavian journal of forest research,* 20**,** 223-234.

HALADA, L., EVANS, D., ROMÃO, C. & PETERSEN, J.-E. 2011. Which habitats of European importance depend on agricultural practices? *Biodiversity and Conservation,* 20**,** 2365-2378.

HALLMANN, C. A., SORG, M., JONGEJANS, E., SIEPEL, H., HOFLAND, N., SCHWAN, H., STENMANS, W., MÜLLER, A., SUMSER, H., HÖRREN, T., GOULSON, D. & DE KROON, H. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE,* 12**,** e0185809.

HARRISON, P. A., VANDEWALLE, M., SYKES, M. T., BERRY, P. M., BUGTER, R., DE BELLO, F., FELD, C. K., GRANDIN, U., HARRINGTON, R. & HASLETT, J. R. 2010. Identifying and prioritising services in European terrestrial and freshwater ecosystems. *Biodiversity and Conservation,* 19**,** 2791-2821.

HARTEL, T., DORRESTEIJN, I., KLEIN, C., MÁTHÉ, O., MOGA, C. I., ÖLLERER, K., ROELLIG, M., VON WEHRDEN, H. & FISCHER, J. 2013. Wood-pastures in a traditional rural region of Eastern Europe: Characteristics, management and status. *Biological Conservation,* 166**,** 267-275.

HARTEL, T., PLIENINGER, T. & VARGA, A. 2015. Wood-pastures in Europe. *In:* KIRBY, K. J. & WATKINS, C. (eds.) *Europe's Changing Woods and Forests: From Wildwood to Cultural Landscapes.* CAB International.

HARTIG, T., MITCHELL, R., DE VRIES, S. & FRUMKIN, H. 2014. Nature and health. *Annual review of public health,* 35**,** 207-228.

HARTIG, T., VAN DEN BERG, A. E., HAGERHALL, C. M., TOMALAK, M., BAUER, N., HANSMANN, R., OJALA, A., SYNGOLLITOU, E., CARRUS, G., VAN HERZELE, A., BELL, S., PODESTA, M. T. C. & WAASETH, G. 2011. Health Benefits of Nature Experience: Psychological, Social and Cultural Processes. *In:* NILSSON, K., SANGSTER, M., GALLIS, C., HARTIG, T., DE VRIES, S., SEELAND, K. & SCHIPPERIJN, J. (eds.) *Forests, Trees and Human Health.* Dordrecht: Springer Netherlands.

HAY, R. 1998. Sense of place in developmental context. *Journal of environmental psychology,* 18**,** 5-29.

HAYNES, G. 2012. Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology,* 157**,** 99-107.

HEIN, L., VAN KOPPEN, K., DE GROOT, R. S. & VAN IERLAND, E. C. 2006. Spatial scales, stakeholders and the valuation of ecosystem services. *Ecological Economics,* 57**,** 209-228.

HELLSTRÖM, K., HUHTA, A.-P., RAUTIO, P., TUOMI, J., OKSANEN, J. & LAINE, K. 2003. Use of sheep grazing in the restoration of semi-natural meadows in northern Finland. *Applied vegetation science,* 6**,** 45-52.

HENNEKE, D., POTTER, G., KREIDER, J. & YEATES, B. 1983. Relationship between condition score, physical measurements and body fat percentage in mares. *Equine veterinary journal,* 15**,** 371-372.

HEVIA, V., AZCÁRATE, F., OTEROS-ROZAS, E. & GONZÁLEZ, J. 2013. Exploring the role of transhumance drove roads on the conservation of ant diversity in Mediterranean agroecosystems. *Biodiversity and Conservation,* 22**,** 2567-2581.

HOLM, J. A., THOMPSON, J. R., MCSHEA, W. J. & BOURG, N. A. 2013. Interactive effects of chronic deer browsing and canopy gap disturbance on forest successional dynamics. *Ecosphere,* 4**,** 1-23.

HOOPER, D. U., ADAIR, E. C., CARDINALE, B. J., BYRNES, J. E., HUNGATE, B. A., MATULICH, K. L., GONZALEZ, A., DUFFY, J. E., GAMFELDT, L. & O'CONNOR, M. I. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature,* 486**,** 105-108.

HOPCRAFT, J. G. C., OLFF, H. & SINCLAIR, A. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution,* 25**,** 119-128.

HUNT, R., HODGSON, J. G., THOMPSON, K., BUNGENER, P., DUNNETT, N. P., ASKEW, A. P. & BAKKER, J. P. 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science,* 7**,** 163-170.

HUNTSINGER, L. & OVIEDO, J. L. 2014. Ecosystem Services are Social-ecological Services in a Traditional Pastoral System: the Case of California's Mediterranean Rangelands. *Ecology and Society,* 19.

HUNZIKER, M., BUCHECKER, M. & HARTIG, T. 2007. Space and Place – Two Aspects of the Human-landscape Relationship. *In:* KIENAST, F., WILDI, O. & GHOSH, S. (eds.) *A Changing World. Challenges for Landscape Research.* Springer.

HÖRNBERG, S. 2001. The relationship between moose (Alces alces) browsing utilisation and the occurrence of different forage species in Sweden. *Forest Ecology and Management,* 149**,** 91-102.

JOFFRE, R., VACHER, J., DE LOS LLANOS, C. & LONG, G. 1988. The dehesa: an agrosilvopastoral system of the Mediterranean region with special reference to the Sierra Morena area of Spain. *Agroforestry Systems,* 6**,** 71-96.

JØRGENSEN, D. 2013. Pigs and pollards: medieval insights for UK wood pasture restoration. *Sustainability,* 5**,** 387-399.

JØRGENSEN, D. & QUELCH, P. 2014. The origins and history of medieval wood-pastures. *In:* HARTEL, T. & PLIENINGER, T. (eds.) *European Wood-pastures in Transition. A social-ecological approach.* Oxon and New York: Routledge.

KAPLAN, R. & KAPLAN, S. 1989. *The Experience of Nature,* Cambridge: University Press.

KLEIN, J. 1920. *The Mesta: a study in Spanish economic history 1273-1836,* Cambridge, UK, Cambridge University Press.

KLEYER, M., BEKKER, R., KNEVEL, I., BAKKER, J., THOMPSON, K., SONNENSCHEIN, M., POSCHLOD, P., VAN GROENENDAEL, J., KLIMEŠ, L. & KLIMEŠOVÁ, J. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology,* 96**,** 1266-1274.

KLOTZ, S., KÜHN, I. & DURKA, W. 2002. BIOFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde,* 38**,** 1-334.

KNAPP, A. K., BLAIR, J. M., BRIGGS, J. M., COLLINS, S. L., HARTNETT, D. C., JOHNSON, L. C. & TOWNE, E. G. 1999. The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience,* 49**,** 39-50.

KOMONEN, A., GRAPPUTO, A., KAITALA, V., KOTIAHO, J. S. & PÄIVINEN, J. 2004. The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos,* 105**,** 41-54.

KORPELA, K. M., HARTIG, T., KAISER, F. G. & FUHRER, U. 2001. Restorative experience and self-regulation in favorite places. *Environment and behavior,* 33**,** 572-589.

KRAHULEC, F., SKÁLOVÁ, H., HERBEN, T., HADINCOVÁ, V., WILDOVÁ, R. & PECHÁČKOVÁ, S. 2001. Vegetation changes following sheep grazing in abandoned mountain meadows. *Applied Vegetation Science,* 4**,** 97-102.

KREBS, J. R., WILSON, J. D., BRADBURY, R. B. & SIRIWARDENA, G. M. 1999. The second silent spring? *Nature,* 400**,** 611-612.

KREMEN, C., WILLIAMS, N. M., AIZEN, M. A., GEMMILL-HERREN, B., LEBUHN, G., MINCKLEY, R., PACKER, L., POTTS, S. G., STEFFAN-DEWENTER, I. & VÁZQUEZ, D. P. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology letters,* 10**,** 299-314.

KSLA 1998. *Det svenska jordbrukets historia,* Sweden, Fembladsverket. Kungliga skogs- och lantbruksakademin.

KUITERS, A. T. & SLIM, P. A. 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. *Biological Conservation,* 105**,** 65-74.

LALIBERTE, E., SHIPLEY, B., NORTON, D. A. & SCOTT, D. 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology,* 100**,** 662-677.

LANDIS, D. A. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology,* 18**,** 1-12.

LAVOREL, S. & GARNIER, É. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology,* 16**,** 545-556.

LAVOREL, S., GRIGULIS, K., MCINTYRE, S., WILLIAMS, N. S., GARDEN, D., DORROUGH, J., BERMAN, S., QUÉTIER, F., THÉBAULT, A. & BONIS, A. 2008. Assessing functional diversity in the field–methodology matters! *Functional Ecology,* 22**,** 134-147.

LEZAMA, F., BAEZA, S., ALTESOR, A., CESA, A., CHANETON, E. J. & PARUELO, J. M. 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science,* 25**,** 8-21.

LILJEGREN, R. & EKSTRÖM, J. 1996. The terrestrial Late Glacial fauna in south Sweden. *In:* LARSON, L. (ed.) *The Earliest Settlement of Scandinavia.* Lund: Acta Archaeologica Lundensia.

LINDBLADH, M. & FOSTER, D. R. 2010. Dynamics of long-lived foundation species: the history of Quercus in southern Scandinavia. *Journal of Ecology,* 98**,** 1330-1345.

LJUNGGREN, B. 1967. *Stambok för russ,* Gotland, Gotlands Läns Hushållningssällskap.

LÓPEZ-SÁNCHEZ, A., SAN MIGUEL, A., LÓPEZ-CARRASCO, C., HUNTSINGER, L. & ROIG, S. 2016. The important role of scattered trees on the herbaceous diversity of a grazed Mediterranean dehesa. *Acta Oecologica,* 76**,** 31-38.

LÓPEZ SÁEZ, J. A., LÓPEZ GARCÍA, P., LÓPEZ-MERINO, L., CERRILLO CUENCA, E., GONZÁLEZ CORDERO, A. & PRADA GALLARDO, A. 2007. Origen prehistórico de la dehesa en Extremadura: una perspectiva paleoambiental. *Revista de estudios extremeños,* 63**,** 493-510.

LÄTTMAN, H., BERGMAN, K.-O., RAPP, M., TÄLLE, M., WESTERBERG, L. & MILBERG, P. 2014. Decline in lichen biodiversity on oak trunks due to urbanization. *Nordic Journal of Botany,* 32**,** 518-528.

MA 2005. *Millenium Ecosystem Assessment. Ecosystems and Human Well-being: Synthesis Report*, Island Press.

MARAÑÓN, T. 1985. Diversidad florística y heterogeneidad ambiental en una dehesa de Sierra Morena. *Floristic diversity and environmental heterogeneity in "dehesa" of Sierra Morena*.

MARAÑÓN, T. 1988. Agro-Sylvo-Pastoral Systems in the Iberian Peninsula: Dehesas and Montados. *Rangelands,* 10**,** 255-258.

MARSH, G. P. & LOWENTHAL, D. 1965. *Man and nature,* University of Washington Press.

MARTÍN-LÓPEZ, B., GÓMEZ-BAGGETHUN, E., LOMAS, P. L. & MONTES, C. 2009a. Effects of spatial and temporal scales on cultural services valuation. *Journal of Environmental Management,* 90**,** 1050-1059.

MARTÍN-LÓPEZ, B., INIESTA-ARANDIA, I., GARCÍA-LLORENTE, M., PALOMO, I., CASADO-ARZUAGA, I., AMO, D. G. D., GÓMEZ-BAGGETHUN, E., OTEROS-ROZAS, E., PALACIOS-AGUNDEZ, I., WILLAARTS, B., GONZÁLEZ, J. A., SANTOS-MARTÍN, F., ONAINDIA, M., LÓPEZ-SANTIAGO, C. & MONTES, C. 2012. Uncovering Ecosystem Service Bundles through Social Preferences. *PLoS ONE,* 7**,** e38970.

MARTÍN-LÓPEZ, B., MONTES, C., RAMÍREZ, L. & BENAYAS, J. 2009b. What drives policy decision-making related to species conservation? *Biological Conservation,* 142**,** 1370-1380.

MARTIN, J.-L., STOCKTON, S. A., ALLOMBERT, S. & GASTON, A. J. 2010. Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biological Invasions,* 12**,** 353-371.

MARULL, J., TELLO, E., FULLANA, N., MURRAY, I., JOVER, G., FONT, C., COLL, F., DOMENE, E., LEONI, V. & DECOLLI, T. 2015. Long-term bio-cultural heritage: exploring the intermediate disturbance hypothesis in agro-ecological landscapes (Mallorca, c. 1850–2012). *Biodiversity and conservation,* 24**,** 3217-3251.

MASCIA, M. B., BROSIUS, J. P., DOBSON, T. A., FORBES, B. C., HOROWITZ, L., MCKEAN, M. A. & TURNER, N. J. 2003. Conservation and the Social Sciences. *Conservation Biology,* 17**,** 649-650.

MCCULLOCH, C. E. & NEUHAUS, J. M. 2001. *Generalized linear mixed models,* Wiley Online Library.

MILBERG, P., BERGMAN, K.-O., CRONVALL, E., ERIKSSON, Å. I., GLIMSKÄR, A., ISLAMOVIC, A., JONASON, D., LÖFQVIST, Z. & WESTERBERG, L. 2016. Flower abundance and vegetation height as predictors for nectar-feeding insect occurrence in Swedish semi-natural grasslands. *Agriculture, Ecosystems & Environment,* 230**,** 47-54.

MORENO, G., GONZALEZ-BORNAY, G., PULIDO, F., LOPEZ-DIAZ, M. L., BERTOMEU, M., JUÁREZ, E. & DIAZ, M. 2016. Exploring the causes of high biodiversity of Iberian dehesas: the importance of wood pastures and marginal habitats. *Agroforestry Systems,* 90**,** 87-105.

MORENO, G. & PULIDO, F. 2009. The Functioning, Management and Persistence of Dehesas. *In:* RIGUEIRO-RODRÍGUEZ, A., MCADAM, J. & MOSQUERA-LOSADA, M. R. (eds.) *Agroforestry in Europe. Current Status and Future Prospects.* Springer.

MORETTI, M., DE BELLO, F., ROBERTS, S. P. & POTTS, S. G. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology,* 78**,** 98-108.

MOSQUERA-LOSADA, M. R., MCADAM, J. H., ROMERO-FRANCO, R., SANTIAGO-FREIJANES, J. J. & RIGUEIRO-RODRÍGUEZ, A. 2009. Definitions and Components of Agroforestry Practices in Europe. *In:* RIGUEIRO-RODRÍGUEZ, A., MCADAM, J. H. & MOSQUERA-LOSADA, M. R. (eds.) *Agroforestry in Europe. Current Status and Future Prospects.* Springer.

MUIR, J. 1901. *Our national parks,* Houghton Mifflin.

MÅNSSON, J., KALÉN, C., KJELLANDER, P., ANDRÉN, H. & SMITH, H. 2007. Quantitative estimates of tree species selectivity by moose (Alces alces) in a forest landscape. *Scandinavian Journal of Forest Research,* 22**,** 407-414.

NICHOLS, R. V., CROMSIGT, J. P. G. M. & SPONG, G. 2015. DNA left on browsed twigs uncovers bite-scale resource use patterns in European ungulates. *Oecologia,* 178**,** 275-284.

O'FARRELL, P. J. & ANDERSON, P. M. 2010. Sustainable multifunctional landscapes: a review to implementation. *Current Opinion in Environmental Sustainability,* 2**,** 59-65.

OLEA, L. & SAN MIGUEL, A. The Spanish dehesa. A traditional Mediterranean silvopastoral system linking production and nature conservation. 21st General Meeting of the European Grassland Federation, 2006 Badajoz (Spain).

OPPERMANN, R., BEAUFOY, G. & JONES, G. 2012. High Nature Value Farming in Europe - 35 European Countries, Experiences and Perspectives. Verlag Regionalkultur, Ubstadt-Weiher.

ORIANS, G. H. 1980. Habitat selection: General theory and applications to human behavior. *In:* LOCKARD, G. S. (ed.) *The evolution of human social behavior.* New York: Elsevier.

OTEROS-ROZAS, E., GONZÁLEZ, J., MARTÍN-LÓPEZ, B., LÓPEZ, C. & MONTES, C. 2012. Ecosystem services and social-ecological resilience in transhumance cultural landscapes: learning from the past, looking for a future. *Resilience and the Cultural*

*Landscape. Understanding and Managing Change in Human-shaped Environments'.(Eds T. Plieninger and C. Bieling.) pp***,** 242-260.

OTEROS-ROZAS, E., MARTÍN-LÓPEZ, B., GONZÁLEZ, J., PLIENINGER, T., LÓPEZ, C. & MONTES, C. 2014. Socio-cultural valuation of ecosystem services in a transhumance social-ecological network. *Regional Environmental Change,* 14**,** 1269-1289.

OWEN-SMITH, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology,* 13**,** 351-362.

PALMER, S. C. F. & TRUSCOTT, A. M. 2003. Browsing by deer on naturally regenerating Scots pine (Pinus sylvestris L.) and its effects on sapling growth. *Forest Ecology and Management,* 182**,** 31-47.

PALOMO, I., FELIPE-LUCIA, M. R., BENNETT, E. M., MARTÍN-LÓPEZ, B. & PASCUAL, U. 2016. Disentangling the pathways and effects of ecosystem service co-production. *In:* GUY, W. & DAVID, A. B. (eds.) *Advances in Ecological Research.* Academic Press.

PALTTO, H., NORDBERG, A., NORDEN, B. & SNÄLL, T. 2011. Development of Secondary Woodland in Oak Wood Pastures Reduces the Richness of Rare Epiphytic Lichens. *Plos One,* 6**,** e24675.

PALTTO, H., THOMASSON, I. & NORDEN, B. 2010. Multispecies and multiscale conservation planning: setting quantitative targets for red-listed lichens on ancient oaks. *Conserv Biol,* 24**,** 758-68.

PARSONS, J. J. 1962. The acorn-hog economy of the oak woodlands of southwestern Spain. *Geographical Review* 52**,** 211-235.

PELTZER, D. A., ALLEN, R. B., BELLINGHAM, P. J., RICHARDSON, S. J., WRIGHT, E. F., KNIGHTBRIDGE, P. I. & MASON, N. W. 2014. Disentangling drivers of tree population size distributions. *Forest Ecology and Management,* 331**,** 165-179.

PEREIRA, H. M., LEADLEY, P. W., PROENÇA, V., ALKEMADE, R., SCHARLEMANN, J. P., FERNANDEZ-MANJARRÉS, J. F., ARAÚJO, M. B., BALVANERA, P., BIGGS, R. & CHEUNG, W. W. 2010. Scenarios for global biodiversity in the 21st century. *Science,* 330**,** 1496-1501.

PÉREZ-HARGUINDEGUY, N., DÍAZ, S., CORNELISSEN, J. H., VENDRAMINI, F., CABIDO, M. & CASTELLANOS, A. 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil,* 218**,** 21-30.

PLIENINGER, T. & BIELING, C. 2012. *Resilience and the cultural landscape: understanding and managing change in human-shaped environments*, Cambridge University Press.

PLIENINGER, T. & BIELING, C. 2013. Resilience-Based Perspectives to Guiding High-Nature-Value Farmland through Socioeconomic Change. *Ecology and Society,* 18.

PLIENINGER, T., BIELING, C., FAGERHOLM, N., BYG, A., HARTEL, T., HURLEY, P., LÓPEZ-SANTIAGO, C. A., NAGABHATLA, N., OTEROS-ROZAS, E., RAYMOND, C. M., VAN DER HORST, D. & HUNTSINGER, L. 2015a. The role of cultural ecosystem services in landscape management and planning. *Current Opinion in Environmental Sustainability,* 14**,** 28-33.

PLIENINGER, T., DIJKS, S., OTEROS-ROZAS, E. & BIELING, C. 2013. Assessing, mapping, and quantifying cultural ecosystem services at community level. *Land Use Policy,* 33**,** 118-129.

PLIENINGER, T., HARTEL, T., MARTÍN-LÓPEZ, B., BEAUFOY, G., BERGMEIER, E., KIRBY, K., MONTERO, M. J., MORENO, G., OTEROS-ROZAS, E. & VAN UYTVANCK, J. 2015b. Wood-pastures of Europe: Geographic coverage, social–ecological values, conservation management, and policy implications. *Biological Conservation,* 190**,** 70-79.

PLIENINGER, T., PULIDO, F. J. & SCHAICH, H. 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in Quercus ilex L. dehesas. *Journal of Arid Environments,* 57**,** 345-364.

POLLOCK, M. L., MILNER, J. M., WATERHOUSE, A., HOLLAND, J. P. & LEGG, C. J. 2005. Impacts of livestock in regenerating upland birch woodlands in Scotland. *Biological Conservation,* 123**,** 443-452.

PRESCOTT, G. W., WILLIAMS, D. R., BALMFORD, A., GREEN, R. E. & MANICA, A. 2012. Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions. *Proceedings of the National Academy of Sciences,* 109**,** 4527-4531.

PULIDO, F., PICARDO, A., CAMPOS, P., CARRANZA, J., COLETO, J. M., DÍAZ, M., DIÉGUEZ, E., ESCUDERO, A., EZQUERRA, F. J., FERNÁNDEZ, P., LÓPEZ, L., MONTERO, G., MORENO, G., OLEA, L., ROIG, S., SÁNCHEZ, E., SOLLA, A., VARGAS, J. D. & VIDIELLA, A. 2010. *Libro Verde de la Dehesa. Documento para el debate hacia un Estrategia Ibérica de gestión,* Salamanca.

PYKÄLÄ, J. 2003. Effects of restoration with cattle grazing on plant species composition and richness of semi-natural grasslands. *Biodiversity & Conservation,* 12**,** 2211-2226.

PYKÄLÄ, J. 2005. Plant species responses to cattle grazing in mesic semi-natural grassland. *Agriculture, Ecosystems & Environment,* 108**,** 109-117.

PYKÄLÄ, J., LUOTO, M., HEIKKINEN, R. K. & KONTULA, T. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic and applied Ecology,* 6**,** 25-33.

PÄIVIÖ, E.-L. 2008. *Det agrara landskapet på vinst och förlust. Biologiska och historiska värden inom lantbrukets nya uppdrag.* Doctoral thesis No. 2008:95, Swedish University of Agricultural Sciences.

PÖYRY, J., LINDGREN, S., SALMINEN, J. & KUUSSAARI, M. 2004. Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications,* 14**,** 1656-1670.

QUÉTIER, F., RIVOAL, F., MARTY, P., DE CHAZAL, J., THUILLER, W. & LAVOREL, S. 2010. Social representations of an alpine grassland landscape and socio-political discourses on rural development. *Regional Environmental Change,* 10**,** 119-130.

RACKHAM, O. 2008. Ancient woodlands: modern threats. *New Phytologist,* 180**,** 571-586.

RANIUS, T., AGUADO, L. O., ANTONSSON, K., AUDISIO, P., BALLERIO, A., CARPANETO, G. M., CHOBOT, K., GJURASIN, B., HANSSEN, O., HUIJBREGTS, H., LAKATOS, F., MARTIN, O., NECULISEANU, Z., NIKITSKY, N. B., PAILL, W., PIRNAT, A., RIZUN, V., RUICANESCU, A., STEGNER, J., SDA, I., SZWALKO, P.,

TAMUTIS, V., TELNOV, D., TSINKEVICH, V., VERSTEIRT, V., VIGNON, V., VÖGELI, M. & ZACH, P. 2005. Osmoderma eremita (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. *Animal Biodiversity and Conservation,* 28.1.

REICH, P. B., WRIGHT, I. J. & LUSK, C. H. 2007. Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecological Applications,* 17**,** 1982-1988.

RIBEIRO, S. M. C., CORREIA, T. P. & PARACCHINI, M. L. 2016. Addressing the social landscape dimensions: The need for reconciling cross scale assessments for capturing Cultural Ecosystem Services (CES). *Land Use Policy,* 53**,** 1-2.

RIPPLE, W. J., CHAPRON, G., LÓPEZ-BAO, J. V., DURANT, S. M., MACDONALD, D. W., LINDSEY, P. A., BENNETT, E. L., BESCHTA, R. L., BRUSKOTTER, J. T. & CAMPOS-ARCEIZ, A. 2017. Conserving the World's Megafauna and Biodiversity: The Fierce Urgency of Now. *Bioscience,* 67**,** 197-200.

RIPPLE, W. J., ESTES, J. A., BESCHTA, R. L., WILMERS, C. C., RITCHIE, E. G., HEBBLEWHITE, M., BERGER, J., ELMHAGEN, B., LETNIC, M. & NELSON, M. P. 2014. Status and ecological effects of the world's largest carnivores. *Science,* 343**,** 1241484.

SANDOM, C., FAURBY, S., SANDEL, B. & SVENNING, J.-C. Global late Quaternary megafauna extinctions linked to humans, not climate change. Proc. R. Soc. B, 2014. The Royal Society, 20133254.

SATTERFIELD, T., GREGORY, R., KLAIN, S., ROBERTS, M. & CHAN, K. M. 2013. Culture, intangibles and metrics in environmental management. *Journal of Environmental Management,* 117**,** 103-114.

SBA 2005a. Svenskt jordbruk i siffror 1800–2004. Jönköping: Swedish Board of Agriculture [Jordsbruksverket].

SBA 2005b. Ängs- och betesmarksinventeringen 2002–2004. Jönköping: Swedish Board of Agriculture [Jordsbruksverket].

SCHOLTE, S. S. K., VAN TEEFFELEN, A. J. A. & VERBURG, P. H. 2015. Integrating socio-cultural perspectives into ecosystem service valuation: A review of concepts and methods. *Ecological Economics,* 114**,** 67-78.

SJÖDIN, N. E., BENGTSSON, J. & EKBOM, B. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology,* 45**,** 763-772.

SOHEL, M. S. I., AHMED MUKUL, S. & BURKHARD, B. 2015. Landscape′s capacities to supply ecosystem services in Bangladesh: A mapping assessment for Lawachara National Park. *Ecosystem Services,* 12**,** 128-135.

STRAUSS, S. Y. & AGRAWAL, A. A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution,* 14**,** 179-185.

SVENNING, J.-C., PEDERSEN, P. B. M., DONLAN, C. J., EJRNÆS, R., FAURBY, S., GALETTI, M., HANSEN, D. M., SANDEL, B., SANDOM, C. J., TERBORGH, J. W. & VERA, F. W. M. 2016. Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences,* 113**,** 898-906.

SVENSSON, R. 1988. Floravård i jordbrukslandskapet (Flora conservation in the agricultural landscape). *Svensk botanisk tidskrift,* 82**,** 458–465.

SZÜCS, L., ANDERS, U. & BÜRGER-ARNDT, R. 2015. Assessment and illustration of cultural ecosystem services at the local scale – A retrospective trend analysis. *Ecological Indicators,* 50**,** 120-134.

TACCONI, L. 2000. *Biodiversity and Ecological Economics. Participation, Values, and Resource Management,* London, Earthscan.

TAKATSUKI, S. 2009. Effects of sika deer on vegetation in Japan: A review. *Biological Conservation,* 142**,** 1922-1929.

TEEB 2010. The Economics of Ecosystems and Biodiversity: Mainstreaming the Economics of Nature: A synthesis of the approach, conclusions and recommendations of TEEB.

TENGBERG, A., FREDHOLM, S., ELIASSON, I., KNEZ, I., SALTZMAN, K. & WETTERBERG, O. 2012. Cultural ecosystem services provided by landscapes: assessment of heritage values and identity. *Ecosystem Services,* 2**,** 14-26.

THOMAS, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 360**,** 339-357.

THOMAS, J. A., TELFER, M. G., ROY, D. B., PRESTON, C. D., GREENWOOD, J., ASHER, J., FOX, R., CLARKE, R. T. & LAWTON, J. H. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science,* 303**,** 1879-1881.

TIESKENS, K. F., SCHULP, C. J., LEVERS, C., LIESKOVSKÝ, J., KUEMMERLE, T., PLIENINGER, T. & VERBURG, P. H. 2017. Characterizing European cultural landscapes: Accounting for structure, management intensity and value of agricultural and forest landscapes. *Land Use Policy,* 62**,** 29-39.

TILGHMAN, N. G. 1989. Impacts of White-Tailed Deer on Forest Regeneration in Northwestern Pennsylvania. *The Journal of Wildlife Management,* 53**,** 524-532.

TORRALBA, M., FAGERHOLM, N., BURGESS, P. J., MORENO, G. & PLIENINGER, T. 2016. Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis. *Agriculture, Ecosystems & Environment,* 230**,** 150-161.

TORRALBA, M., OTEROS-ROZAS, E., MORENO, G. & PLIENINGER, T. 2017. Exploring the Role of Management in the Coproduction of Ecosystem Services from Spanish Wooded Rangelands. *Rangeland Ecology & Management*.

TSCHARNTKE, T., TYLIANAKIS, J. M., RAND, T. A., DIDHAM, R. K., FAHRIG, L., BATARY, P., BENGTSSON, J., CLOUGH, Y., CRIST, T. O. & DORMANN, C. F. 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological Reviews,* 87**,** 661-685.

TUAN, Y. F. 1977. *Space and place,* London, Arnold.

TÄLLE, M., DEÁK, B., POSCHLOD, P., VALKÓ, O., WESTERBERG, L. & MILBERG, P. 2016. Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. *Agriculture, Ecosystems & Environment,* 222**,** 200-212.

ULRICH, R. S. 1983. Aesthetic and affective response to natural environment. *In:* ALTMAN, I. & WOHLWILL, J. F. (eds.) *Behavior and the natural environment.* New York: Plenum Press.

VALIENTE-BANUET, A., AIZEN, M. A., ALCÁNTARA, J. M., ARROYO, J., COCUCCI, A., GALETTI, M., GARCÍA, M. B., GARCÍA, D., GÓMEZ, J. M. & JORDANO, P. 2015.

Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology,* 29**,** 299-307.

WALLISDEVRIES, M. F., POSCHLOD, P. & WILLEMS, J. H. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation,* 104**,** 265-273.

VAN KLINK, R., VAN DER PLAS, F., VAN NOORDWIJK, C., WALLISDEVRIES, M. F. & OLFF, H. 2015. Effects of large herbivores on grassland arthropod diversity. *Biological Reviews,* 90**,** 347-366.

VAN VALKENBURGH, B., HAYWARD, M. W., RIPPLE, W. J., MELORO, C. & ROTH, V. L. 2016. The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences,* 113**,** 862-867.

WARD, A. I., WHITE, P. C., WALKER, N. J. & CRITCHLEY, C. H. 2008. Conifer leader browsing by roe deer in English upland forests: Effects of deer density and understorey vegetation. *Forest Ecology and Management,* 256**,** 1333-1338.

WARDLE, D. A., BARDGETT, R. D., KLIRONOMOS, J. N., SETÄLÄ, H., VAN DER PUTTEN, W. H. & WALL, D. H. 2004. Ecological linkages between aboveground and belowground biota. *Science,* 304**,** 1629-1633.

VELASCO, M. J. P. 2008. *Naturbanization: new identities and processes for rural-natural areas*, CRC Press.

WESTOBY, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil,* 199**,** 213-227.

WESTOBY, M., ELDRIDGE, D. & FREUDENBERGER, D. The LHS strategy scheme in relation to grazing and fire. Proceedings of the VIth International Rangeland Congress, 1999. International Rangeland Congress Townsville, AU, 893-896.

WESTOBY, M., FALSTER, D. S., MOLES, A. T., VESK, P. A. & WRIGHT, I. J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual review of ecology and systematics,* 33**,** 125-159.

WHITE, M. A. 2012. Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest. *Forest Ecology and Management,* 269**,** 222-228.

VIHERVAARA, P., RÖNKÄ, M. & WALLS, M. 2010. Trends in Ecosystem Service Research: Early Steps and Current Drivers. *AMBIO,* 39**,** 314-324.

WILKINSON, C., SAARNE, T., PETERSON, G. D. & COLDING, J. 2013. Strategic Spatial Planning and the Ecosystem Services Concept – an Historical Exploration. *Ecology and Society,* 18**,** 37.

VILLAMOR, G., PALOMO, I., SANTIAGO, C., OTEROS-ROZAS, E. & HILL, J. 2014. Assessing stakeholders' perceptions and values towards social-ecological systems using participatory methods. *Ecological Processes,* 3**,** 1-12.

WILLIAMS, D. R., PATTERSON, M. E., ROGGENBUCK, J. W. & WATSON, A. E. 1992. Beyond the commodity metaphor: Examining emotional and symbolic attachment to place. *Leisure sciences,* 14**,** 29-46.

WILLIAMS, N. M., CRONE, E. E., T'AI, H. R., MINCKLEY, R. L., PACKER, L. & POTTS, S. G. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation,* 143**,** 2280-2291.

WILSON, E. O. 2000. On the future of conservation biology. *Conservation Biology***,** 1-3.

WILSON, J. B., PEET, R. K., DENGLER, J. & PÄRTEL, M. 2012. Plant species richness: the world records. *Journal of vegetation Science,* 23**,** 796-802.

VIOLLE, C., NAVAS, M. L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. 2007. Let the concept of trait be functional! *Oikos,* 116**,** 882-892.

WOLFF, S., SCHULP, C. J. E. & VERBURG, P. H. 2015. Mapping ecosystem services demand: A review of current research and future perspectives. *Ecological Indicators,* 55**,** 159-171.

VON LINNÉ, C. 1745. *Carl Linnæi Öländska och Gotländska resa,* Malmö, Faksimil edition produced 1940, AB Malmö Ljustrycksanstalt, Malmö.

WRIGHT, I. J., REICH, P. B., WESTOBY, M. & ACKERLY, D. D. 2004. The worldwide leaf economics spectrum. *Nature,* 428**,** 821.

ZHENG, S., LI, W., LAN, Z., REN, H. & WANG, K. 2015. Functional trait responses to grazing are mediated by soil moisture and plant functional group identity. 5**,** 18163.

ZHU, H., WANG, D., WANG, L., BAI, Y., FANG, J. & LIU, J. 2012. The effects of large herbivore grazing on meadow steppe plant and insect diversity. *Journal of Applied Ecology,* 49**,** 1075-1083.

ZUUR, A. F., IENO, E. N., WALKER, N. J., SAVELIEV, A. A. & SMITH, G. M. 2009. *Mixed Effects Models and Extensions in Ecology with R,* New York, Springer-Verlag.

ÖCKINGER, E., BERGMAN, K.-O., FRANZÉN, M., KADLEC, T., KRAUSS, J., KUUSSAARI, M., PÖYRY, J., SMITH, H., STEFFAN-DEWENTER, I. & BOMMARCO, R. 2012a. The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology,* 27**,** 121-131.

ÖCKINGER, E., ERIKSSON, A. K. & SMITH, H. G. 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biological Conservation,* 133**,** 291-300.

ÖCKINGER, E., LINDBORG, R., SJÖDIN, N. E. & BOMMARCO, R. 2012b. Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography,* 35**,** 259-267.

ÖCKINGER, E., SCHWEIGER, O., CRIST, T. O., DEBINSKI, D. M., KRAUSS, J., KUUSSAARI, M., PETERSEN, J. D., PÖYRY, J., SETTELE, J., SUMMERVILLE, K. S. & BOMMARCO, R. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters,* 13**,** 969-979.

ØDEGAARD, F., STAVERLØKK, A., GJERSHAUG, J., BENGTSON, R. & MJELDE, A. 2015. *Humler i Norge,* Norsk institutt for naturforskning, Trondheim, Norway, Kjennetegn, utbredelse og levesett.

Popular science summary

How can we better understand wood-pastures to foster conservation? To answer the question it is necessary to investigate both the social and ecological components of wood-pastures.

Wood-pastures combine scattered trees, grasslands and grazing animals. They have been and are part of European cultural landscapes, occur in most regions in Europe, and cover 203 000 km^2. These landscapes have, however, declined due to land use change including both intensification and abandonment of agriculture. Here oak wood-pastures in Sweden ("*eklandskap*") and Spain ("*dehesa*") that are protected by the Habitat Directive of the EU were compared. A standardized research design based on 63 semi-structured interviews with stakeholders at local and regional level of governance was applied. The aim was to map the full range of ecosystem services as perceived by stakeholders, and to compare their perceptions among stakeholders from different sectors and levels of governance in Sweden and Spain.

In Sweden, wood-pastures were traditionally important habitats for the livelihoods of rural people, and were used for animal husbandry and hay-making. Today wood-pastures are valuable habitats for many red-listed saproxylic beetles, butterflies and lichen species that are associated to old sun-exposed oak trees. However, these habitats are severely fragmented, and threatened by the abandonment of traditional land management practices. The best preserved oak wood-pastures in Sweden occur in Östergötland County where they cover around 180 km^2 as scattered small patches. In Spain the wood-pasture landscape (*dehesa*) was used as an agro-silvo-pastoral system for centuries. It has a mosaic structure with a diversity of habitats which hosts specialised and endangered species. Traditional management practices were abandoned in the 1960s, leading to a simplification of land uses. Yet, very large areas remain covered by oak wood-pastures in the Iberian Peninsula, where the province of Cáceres is at the center of the range of the *dehesas*.

Local level perspectives on ecosystem services

Cultural services were the most commonly perceived ecosystem services in Sweden while provisioning services were highlighted the most in Spain. Among cultural services, stakeholders from both regions acknowledged recreation and eco-tourism services associated with wood-pastures. Additionally, cultural landscape and landscape beauty were identified as important in Sweden, whereas in Spain respondents additionally highlighted traditional knowledge and heritage values. Provisioning services included fodder from pastures and meat from livestock, and to a lesser extent timber and crop products in Sweden. In Spain, livestock and pastures were the most mentioned provisioning services, followed by fodder from trees, firewood, charcoal, wild game and many other sub-products such as cheese, olive oil, sausages, and wine. Regarding supporting services, both Swedish and Spanish respondents appreciated biodiversity. In Spain, respondents also acknowledged water cycling, nutrient cycling and photosynthesis. Regulating services were rarely expressed by stakeholders in Sweden; the only two services mentioned were noise regulation and water regulation and purification. The variety of services perceived by Spanish respondents was much greater, and natural hazard regulation was the most frequently acknowledged. Seed dispersal, erosion regulation and climate regulation were also mentioned.

Regional level perspectives on ecosystem services

Swedish and Spanish respondents valued cultural services the most. Swedes mostly mentioned recreation and eco-tourism services, landscape beauty and education and knowledge. Spaniards appreciated most frequently education and knowledge services, traditional knowledge, cultural landscape and recreation and eco-tourism services. Biodiversity, and particularly species richness, as supporting services were highlighted both by Swedish and Spanish respondents at the regional level; as well as primary production services in Spain. Provisioning services were rarely mentioned by Swedish respondents, with timber, fodder and crops being equally named. In contrast, livestock was acknowledged the most, followed by fodder and other services mentioned to much lesser extent by regional level Spanish respondents. Surprisingly, regulating services were not mentioned by any Swedish respondent at regional level, whereas Spanish respondents acknowledged all services but noise regulation; climate regulation, water regulation and purification and natural hazard regulation appeared most frequently.

Current challenges for wood-pasture conservation

Throughout Europe the importance of wood-pasture landscapes has been recognized. However, they are still subject to changing socio-economic processes, and are commonly becoming degraded and fragmented. Current threats such as urban sprawl, land abandonment and agricultural intensification entail even greater uncertainty for the long term conservation of valuable wood-pasture landscapes in Europe. In Sweden, oak wood-pastures are deteriorating due to (1) land abandonment and the absence of livestock, (2) active transformation of agricultural land to Norway spruce plantations, and (3) habitat fragmentation. Additionally, the beauty of the landscape attracts people to live closer to wood-pastures, which promotes further fragmentation of habitats due to urbanization and grey infrastructure (i.e., road development) development. Restoration of wood-pastures is of limited effect unless grazing regimes are maintained and oak regeneration is secured. However, such management practices are of marginal profitability today. Additional constraints are hard work conditions, lack of financial support, as well as the lack of new entrants into farming. Both Spanish and Swedish respondents were concerned about hard working conditions, marginal profitability, and abandonment, transformation or intensification of land. Spanish respondents expressed additional concerns about the loss of traditional knowledge, excessive grazing pressure with negative consequences for tree regeneration; a disease causing tree death (“la seca”); abandonment of traditional practices like transhumance (i.e., traditional seasonal migration of herds from the summer pastures in the north to the winter areas in the south of Spain), and climate change. Institutional factors were also commonly mentioned, including lack of a new specific legal framework for the *dehesa*. Today it falls under the legislation for forestry, agriculture, livestock and environment, which limits integrated management of the *dehesa* system.

Multi-stakeholder collaboration and multifunctional landscape management should be supported, as well as the incorporation of mechanisms facilitating the delivery of local products and markets. This could potentially be achieved by developing Protected Designation of Origin mechanisms. Finally, Payment schemes for Ecosystem Services could be integrated into agri-environmental schemes to compensate farmers for the production of services to society.

Possible solutions for wood-pasture conservation

Current wood-pasture restoration efforts are costly and grazing management regimes of marginal profitability to farmers and therefore alternatives for wood-pasture restoration and management are needed. Large herbivores are an integral component of wood-pastures and may thus be utilized for wood-pasture restoration and management. In Sweden there is a critically endangered horse breed, the Gotland Russ (*Equus ferus caballus* L.), that might have retained a sufficient rustic character to be used for wood-pasture restoration and management. To test whether this horse breed could be used for wood-pasture restoration and management, a three year field experiment with paired control and experimental plots was applied. We specifically tested whether horse browsing had an effect on the forest structure, and on the forest composition, and therefore quantified 1) browsing pressure, 2) tree consumption and 3) tree selectivity estimates. Horses reduced forest structure diversity and affected the tree composition via selective browsing. Browsing pressure ranged from 71 % for ash to 19 % for pine, thus ash had 4 times higher probability of being browsed compared to pine.

Horse grazing also promoted grassland biodiversity by inferring changes in the grassland composition and plant species richness. Additionally grazing had positive effects on butterfly and bumble bee species richness and habitat use, which have positive effects for the functioning of grassland ecosystems. Horses could therefore be used for wood-pasture restauration and management since they have clear effects on the forest structure and composition. This management alternative could promote the generation of additional income for farmers and thus dually support landscape and biodiversity conservation oriented management efforts as well as the preservation of a critically endangered breed.

Populärvetenskaplig sammanfattning

Hur kan vi bättre förstå skogsbetesmarker för att främja dess bevarande? För att kunna svara på den frågan är det nödvändigt att studera både sociala- och ekologiska aspekter av skogsbetesmarker.

Skogsbetesmarker karakteriseras av glest spridda träd, gräsmarker och betesdjur. De har varit och är fortfarande en del av det europeiska kulturlandskapet, förekommer i de flesta regioner i Europa och täcker 203 000 km^2. Dessa kulturlandskap har dock minskat på grund av förändrad markanvändning, både i form av intensifiering och nedläggning av traditionellt jordbruk. I denna studie jämfördes svenska eklandskapet med Spaniens motsvarighet ”*dehesa*”, vilka båda finns upptagna i EU:s habitatdirektiv. En standardiserad forskningsdesign användes, baserad på totalt 63 intervjuer med intressenter på lokal och regional nivå. Syftet var att kartlägga hela spektret av ekosystemtjänster så som de uppfattas av intressenter, och att jämföra intressenter från olika sektorer och nivåer för samhällsstyrning i Sverige och Spanien.

I Sverige var skogsbetesmarker traditionellt viktiga livsmiljöer för landsbygdsbefolkningen och användes för beteshävd och slåtter. Idag är skogsbetesmarker värdefulla livsmiljöer för många hotade vedlevande skalbaggar, samt fjärilar och lavarter som trivs i gamla, solexponerade grova ekar. Dessa livsmiljöer är numera fragmenterade och hotas av att det traditionella brukandet överges. De bäst bevarade eklandskapen i Sverige förekommer som spridda små fläckar i Östergötlands län, där de täcker omkring 180 km^2. I Spanien har eklandskapet använts som ett agro-silvo-pastoralt system under århundraden. Det har en mosaikstruktur med en mångfald av livsmiljöer som hyser specialiserade och hotade arter. Det traditionella brukandet övergavs på 1960-talet, vilket ledde till en förenklad markanvändning. Mycket stora områden på den iberiska halvön täcks dock fortfarande av glesa, betade ekskogar. Centrum av det spanska dehesa-området ligger provinsen Cáceres.

Lokala perspektiv på ekosystemtjänster

Kulturella tjänster var de vanligast upplevda ekosystemtjänsterna i Sverige, medan bidragande tjänster framhölls mest i Spanien. Bland kulturella tjänster framhöll intressenter från båda regionerna rekreations- och ekoturismstjänster. Dessutom identifierades kulturlandskapet och landskapets skönhet som viktiga i Sverige, medan respondenterna i Spanien även framhöll traditionell kunskap och kulturarv. Bidragande ekosystemtjänster omfattade i Sverige foder från betesmarker och kött från boskap, samt i mindre utsträckning timmer och jordbruksgrödor. I Spanien var boskap och betesmark de mest nämnda bidragande tjänsterna, följda av foder från träd, ved, kol och vilt samt många förädlade produkter såsom ost, olivolja, korv och vin. När det gäller stödjande ekosystemtjänster uppskattade både svenska och spanska respondenter biologisk mångfald. I Spanien nämnde respondenterna även kretslopp av vattnet och näringsämnen, samt fotosyntes. Reglerande tjänster uttrycktes sällan av intressenter i Sverige; de enda som nämndes var skydd mot buller samt vattenrening och -reglering. Spanska respondenter framhöll generellt fler ekosystemtjänster, varav skydd mot naturliga faror såsom brand och erosion var de vanligaste. Fröspridning, erosionsskydd och klimatreglering nämndes också.

Regionala perspektiv på ekosystemtjänster

Svenska och spanska respondenter värderade de kulturella tjänsterna mest. Svenskar nämnde mestadels rekreations- och ekoturismtjänster, landskapets skönhet, samt utbildning och kunskap. Spanjorerna uppskattade utbildning och kunskapstjänster, traditionell kunskap, kulturlandskap, rekreation och ekoturism. Biologisk mångfald, särskilt artrikedom, som stödjande ekosystemtjänst betonades av både svenska och spanska respondenter på regional nivå. I Spanien framhölls även primärproduktionstjänster. Försörjande tjänster nämndes sällan av svenska respondenter, men timmer, foder och grödor förekom i lika omfattning. Däremot framhölls i Sverige boskap, följt av foder och andra tjänster som i mindre utsträckning nämndes av regionala spanska respondenter. Överraskande nog nämndes inte reglerande tjänster av någon svensk respondent på regional nivå, medan spanska respondenter omnämnde alla tjänster utom bullerskydd; klimatreglering, vattenreglering, vattenrening samt skydd mot naturkatastrofer nämndes oftast.

Nuvarande utmaningar för bevarande av skogsbetesmarker

Skogsbetesmarkernas betydelse uppmärksammas i hela Europa. De påverkas dock fortfarande negativt av förändrade socio-ekonomiska processer, vilket leder till degradering och fragmentering. Nuvarande hot, såsom urban expansion samt nedläggning och intensifiering av jordbruket, riskerar långsiktigt bevarande av skogsbetesmarkernas biologiska mångfald i Europa. I Sverige försvinner eklandskapet på grund av (1) nedläggning av jordbruk och frånvaro av boskap, (2) aktiv omvandling av jordbruksmark till granplantager och (3) fragmentering. Dessutom attraherar skogsbetesmarker människor som vill bo nära eklandskapet, vilket i sin tur leder till ytterligare fragmentering av dessa miljöer på grund av urbanisering och expansion av grå infrastruktur (som vägar). Restaurering av eklandskap har begränsad effekt om inte betestrycket upprätthålls och ekföryngringen säkras. Sådana skötselmetoder har dock dålig lönsamhet idag. Tillkommande begränsningar är de hårda arbetsvillkoren, avsaknad av ekonomiskt stöd samt svårighet att rekrytera nya brukare. Både spanska och svenska respondenter var oroade över hårda arbetsförhållanden, dålig lönsamhet, och övergivande-, omvandling- eller intensifiering av brukandet. Spanska respondenter uttryckte även oro över förlusten av traditionell kunskap, för hårt betestryck med negativa följder för trädregenerering; en sjukdom som orsakar träd död ("la seca"); upphörande av traditionella vanor såsom transhumans (dvs säsongsmässig förflyttning av människor och deras boskap mellan fasta sommarområden i Pyrenéerna i norra Spanien och vinterområden i södra Spanien), samt klimatförändringar. Institutionella faktorer nämndes också ofta, inklusive bristen på nya rättsliga regler som är anpassade till mångbruket i *dehesan*. Idag faller *dehesan* under lagstiftning för såväl skogsbruk, jordbruk, boskap och miljö, vilket begränsar en integrerad förvaltning av hela *dehesa*-systemet.

Samverkan mellan intressenter från olika sektorer och multifunktionell landskapsförvaltning behöver stödjas, såväl som mekanismer som underlättar transporten av lokala produkter och -marknader. Det senare kan potentiellt uppnås genom att utveckla skyddade ursprungsbeteckningar. Slutligen kan betalningssystem för ekosystemtjänster integreras i jordbrukets miljöstöd så att jordbrukare får ersättning för sin produktion av tjänster till samhället.

Möjliga lösningar för skogsbetesmarkernas bevarande

Nuvarande ansträngningar för att restaurera skogsbetesmarker är dyra och beteshävd är marginellt lönsamt för bonden. Därför behövs alternativ till dagens restaurering- och förvaltning av skogsbetesmarkerna. Stora växtätare är en integrerad del av skogsbetesmarkerna och kan därför användas som ett redskap. I Sverige finns en hotad lantras, gotlandsrusset (*Equus ferus caballus* L.), som kan ha bevarat rustika egenskaper som lämpar sig för detta ändamål. För att testa detta utfördes ett treårigt fältförsök med parade kontroll- och försöksytor. Vi testade hur hästarnas bete påverkade skogens struktur och sammansättning, och kvantifierade 1) betestryck, 2) trädbete och 3) trädval. Hästarna reducerade skogens strukturella diversitet och påverkade trädsammansättningen genom ett selektivt betestryck. Betestrycket varierade mellan 71% för ask till 19% för tall; det var alltså fyra gånger högre sannolikhet för en ask att betas än en tall.

Hästbete gynnade även gräsmarkernas biodiversitet genom att orsaka förändringar i gräsmarkernas komposition och växtsamhällets artrikedom. Betet hade även positiva effekter på artrikedom och habitatnyttjande av fjärilar och humlor, vilket är gynnsamt för gräsmarkernas ekosystem. Hästar kan därför lämpa sig för restaurering och förvaltning av skogsbetesmarker, i synnerhet som de även har en tydlig effekt på skogens struktur och sammansättning. Detta förvaltningsalternativ kan generera nya former av inkomster för brukare, stödja landskaps- och biodiversitetsinriktade förvaltningssansträngningar samt främja bevarandet av en hotad lantras, gotlandsrusset.

Acknowledgements

In this long journey I need to thank first to my Licentiate supervisors, Marine Elbakidze, Per Angelstam and Robert Axelsson for giving me the chance to enrol the PhD education at SLU. Secondly, to the School of Forest Management and my PhD supervisors, Carl-Gustaf Thulin, Anna Jansson, Anna Skarin and Grzegorz Mikusinski for welcoming me into an ongoing project so I could finish my PhD education. Calle thanks for your determination in searching for funding and, in general for EVERYTHING. Grzegorz, thanks for supporting me in the dark and bright days. Annas, thanks for inviting me to discuss how I could use the russ data to finish my PhD.

Thanks to all stakeholders both from Spain and Sweden with whom I could learn about the complexity of ancient social-ecological systems, practices, cultures, species... The list is quite extensive but in Sweden special thanks to Micke Angelstam to help me in everything, to Karl-Olof Berman at Linköping University for introducing me the Swedish case study landscape; to Linköping municipality officials for their patience and time to answer all our questions; to Tommy Ek at CAB Östergötland, to Christer Segersteen for providing first contacts, as well as to all participants form local to national level in Sweden.

In Spain special thanks to Fernando Pulido, Javier Ezquerra and Gerardo Moreno for suggesting places, organizations and people to visit and contact. To Edu for helping me to find farmers at any time, and who by doing so became a friend. At the regional level, special attention deserves Jose Luis del Pozo, Jefe de Servicio de Ordenación y Gestión Forestal, Dirección General de Medio Ambiente, Consejería de Agricultura, Desarrollo Rural, Medio Ambiente y Energía, for his time and help in organizing all meetings at the administration with all departments involved in the management of the dehesa system. To Suso (Jesus Garzón) to invite us to see and experience a day with trashumant herders and share his knowledge and experiences with me. I have to reiterate my deep gratitude to all stakeholders involved in the study to make it possible and fun; many of them deserve special attention but in particular Enrique from dehesa

Casablanca, to Marce (forillo) for his social skills and getting me involved with farmers and the landscape around Aldeanueva, and to Gero, and Miguel, to show me two really good examples of dehesas estates, and many endangered breeds respectively.

Big thanks to the Russprojekt and all people involved. At SLU thanks to Anna Jansson, project leader, welfare/health, to Carl Gustaf Thulin, assistant project leader, biology/ecology, to Margareta Steen, veterinary medicine, to Kristina Dahlborn, physiology, to Lars Edenius, forest ecology and herbivory, to Erik Öckinger, ecology and grazing, to Eva Tydén, parasitology, to Johan Höglund, parasitology, to Anna Skarin, animal movement, landscape ecology, to Sara Ringmark, animal welfare, health & nutrition, and to Clas Tollin, historical data. To the people that took care of the horses, Åsa Ericsson, Ocean Martinet, Hanna Wallsten. Thanks to the people that constructed the experimental enclosures; Jakob Källström, Andreas Grybäck, Lars Edvin Andersson, Jarl Ryberg. Thanks for collecting data for the project so I could use it. For this purpose thanks to Cecilia Rätz, Sofie Fröberg, Linus Söderquist, Ocean Martinet, Karin Näslund, Niklas Adolfsson, and Hans Johansson. Thanks to all the students involved to help in multiple ways.

I have to express also my gratitude to the funding agents to make this happen. To WWF (to Anna Jansson & Carl-Gustaf Thulin), to Helge Ax:son Johnsons stiftelse (to Carl-Gustaf Thulin), to SLU Division of Estate Management (in kind to Anna Jansson & Carl-Gustaf Thulin), and to Extensus Stiftelse for partially supporting some fieldwork.

Thanks to Ewa, Natalka, Mersha, Vladimir and Tommy for the PhD dinners. Thanks to the gym buddies at Gula, for always having a fresh lätöl to share with me. Thanks Vladimir again for all the R working weekends and share that passion with me. I could not have done all this without your kind help. Of course, thanks to Alessia Uboni for being patient with such a crazy guy. Por ayudarme en todo y tener tanta paciencia, especialmente las últimas semanas. Graccie mille di cuore.

Thanks to family and friends both in Spain and Sweden to support my uneven mood swings. To my father, Francisco Javier Garrido López, for long term economic support of my studies and most importantly, for contaminating me with the passion for nature and wildlife. I know there are many anonymous people I have not mentioned, consequently I also thank to everyone that has contributed directly or indirectly to the project and make with their contribution this personal and professional journey come true.

Pablo Garrido, November 2017.

Appendix 1. The interview manual

A. Background information about an interviewee:

- Could you tell us about yourself?
- How long have you been living /working in the area?
- Do you have any special connections to the area?

B. Ecosystem services and land covers: at present

- How do you use the landscape?
- What services/benefits do you obtain from the landscape/region?
- What services/benefits does your community/organisation/association/company get from the landscape/region?
- What services/benefits are the most important for you?
- Are those benefits free of access?
- How valuable are they for your livelihood?
- Does the landscape contain any value important for you?
- And at your community/organisation/association/company level?
- What are your favourite places in the region? Why?
- If you would be asked to rank benefits from ecosystems from the most important to least important for you, how would you rank it?

A researcher has to use a land cover or topographic map to delineate sites on the map (by using pencil or markers) which were pointed out by an interviewee. Each site has to have an index which connects a certain benefit, a site on the map and the data in excel file (ad hoc process).

C. Trends in supply of ecosystem services

- In the past, how the landscape was used?

- What has changed since then?
- What do you think about why those changes have happened?
- Which are the major changes, both positive and negative?
- How would you like to see the landscape in the future?

The final question:

- Whom should we meet to learn more about the region?